Systematic Zoology

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Systematic Zoology

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Species and Systematics

R. B. CLARK

THE aims of systematics are twofold; they are firstly to give names to organisms and secondly to reflect, as far as is possible, the relationships between organisms by arranging them in a hierarchy of families, orders, classes and phyla. Neither function is fulfilled adequately in modern systematics and, as it stands, the science is arbitrary, approximate and unsatisfactory. There are distinguishable groups of organisms which are not differentiated taxonomically and the relationships between organisms are not adequately shown in the present systematic edifice; both of these defects will be discussed in this paper. It is possible to contrive a number of makeshift improvements in taxonomic procedure which will mitigate this situation, but if they are carried to their logical conclusion, as they must be in any exact science, they will result in a ridiculous and unworkable solution. The difficulties with which systematics is faced are fundamental and inherent in taxonomic procedure and the alternative is an entirely new taxonomic procedure which will permit an exact science of systematics to be developed. This will involve the divorcing of the two functions of systematics, but the only solution which appears to offer some promise of permanency seems to be impracticable in the present state of our knowledge. We are thus left with a dilemma; modern systematics is inadequate, but the alterations needed to make it a satisfactory and exact science are beyond our capabilities. While we may be able to do little or nothing about the deficiencies of systematics, it is worth bearing them in mind, for it is only in this way that a solution can be sought and, if one is found, recognised. Furthermore, in this way fruitless discussions which devolve upon the inadequacies of systematics can be avoided.

One of the discussions which has occupied systematists much in the last decade is the validity of the concept of a species. This may be accounted one of the "fruitless discussions" arising out of the deficiencies of systematics. No one has succeeded in defining a species to the satisfaction of all systematists, and the criteria of a species differ in each group of organisms. Without a definition there can be no clear concept and discussions of the validity of the concept are therefore without significance or meaning. That such a discussion could arise can only be attributed to the dual function of systematics, to the ultimate incompatibility of its two aims and, above all, to the fact that a natural phenomenon is being forced to conform with an artificial and inadequate scientific system.

The discussion of the "reality" of a species is from one standpoint artificial and highly academic. It is evident that species do exist. Two specimens of *Nereis virens* are sufficiently alike for any student, any physiologist or any ecologist to identify them with the aid of a taxonomic key; they do so every day. There can be no doubt that for most practical purposes organisms within a group are more like one another than they are like anything else. The differences between varietal groups within a species are not usually of such magnitude as to be of importance to an experimental biologist who uses the organism as a convenient laboratory plant or animal, nor to the ecologist studying certain types of ecological problems. For them the niceties of taxonomy are a foreign field of knowledge and, so far as their own discipline is concerned, are a hindrance rather than a help. This being so, we may reasonably question the justifica-

tion for the discussion of the nature of a species. The answer is, of course, that the concept of a species is different at different levels of investigation and that the quibbles of the taxonomist, while proper at one level of inquiry, are irrelevant at another. This sounds as though the concept of a species should be akin to the physicists' concept of matter, as indeed it is, but this is not generally admitted by taxonomists, nor is it overtly recognised in systematic procedure. The difficulties of systematics spring from the fact that taxonomic procedure is based on a static view of the nature of a species, whereas a species is in fact a dynamic entity.

Before we discuss the theoretical difficulties of systematics, we must first examine some of the practical difficulties which it faces at the moment. These fall into two groups corresponding to the nomenclatorial and the systematic functions of taxonomy.

Problems of Nomenclature

Systematics is not only a science in its own right; it is also the servant of other biological disciplines in that it has to decide what are recognisable species and to give them names for the convenience of physiologists, ecologists and the like. On the whole, the science has fulfilled this task adequately so far. Most of the commoner plants and animals have been given names so that the experimental biologist can repeat the work of another on specimens of an organism answering to the same description and having the same name, without having to collect them from precisely the same population. It is now becoming apparent that he cannot always do this and get the same results, however. In other words, he has been able to find differences between organisms which the taxonomist cannot distinguish, or at any rate, has not distinguished so far. So long as these differences are morphological there is no great taxonomic problem, but physiological and other non-morphological races present a problem which taxonomists have largely ignored in the past, though it cannot be ignored much longer.

No two areas of the geographical range of a species are identical and organisms are so nicely adapted to the conditions prevailing in their environment, that unless one postulates completely random breeding of a species throughout its entire range, which is in most cases unlikely, no two populations of a species can be identical in all respects. The differences may be physiological, morphological, or both, and they may be phenotypic or genotypic in each case. Descriptions and identifications of organisms are necessarily based upon visible, structural features, and, in consequence, populations which show morphological divergences have attracted the greatest attention. Morphological differences between populations in the absence of physiological ones are unlikely, but the converse is quite possible. Fortunately, as far as we know at present, physiological changes are quite often accompanied by minor morphological changes and so it is possible for the systematist to distinguish the populations exhibiting these differences and to name them. *Gammarus* is an amphipod which inhabits fresh, brackish and marine waters and it has been possible to split the genus on morphological grounds into a complex of species and subspecies living in waters of different salinities (Spooner, 1947, 1951). As might be expected, in those few which have been investigated, there are differences in osmoregulatory ability and in respiration rate between species taken from different habitats (Lowenstein, 1935).

There is no reason to suppose that physiological changes are always accompanied by morphological differentiation. Indeed, several examples are known of physiological races which cannot be distinguished on morphological grounds. The "killer" strain of *Paramecium aurelia* has been shown to have a higher rate of respiration than the sensitive strain, from which it differs genetically though not morphologically (Simonsen and Wagten-

donk, 1949). *Drosophila pseudoobscura* and *D. persimilis* are almost indistinguishable morphologically and Reed, Williams and Chadwick (1942) were able to separate the two on morphological grounds only by comparing the ratio of the volume of the thorax to the product of the wing area and the cube of the wing length in each! So subtle a distinction is not of very great use to the taxonomist, but the two species remain distinct in spite of a wide area of geographical overlap (Dobzhansky and Epling, 1944) and they differ in their temperature preferences. Despite their almost identical morphology, which had previously led to the two being regarded as races "A" and "B" of *D. pseudoobscura,* respectively, they differ physiologically and in their behaviour. The pupae of both have the same rate of respiration at 14° C, but *D. pseudoobscura,* which lives in the warmer habitats, has a lower rate of oxygen consumption than *D. persimilis* at 25° C (Dobzhansky and Poulson, 1935). As Mayr and Dobzhansky (1945) observe, too great an emphasis on morphological distinctions between species leads to the untenable situation in which two *Drosophila* which are genetically, physiologically and ethologically distinct and which retain their identity in spite of a wide range of geographical overlap were regarded merely as two strains of a single species. Subsequently to this discussion Rizki (1951) discovered that in fact the two species could be separated on morphological grounds, but this in no way destroys the force of Mayr and Dobzhansky's observation, nor its general pertinence.

The problem of naming physiological races is even more difficult than appears at first sight, however. Physiological differences between populations may be genotypic or phenotypic. The extent to which physiological differences between different populations of the same species are due to accommodation of individuals, rather than to the selection of mutants which are better adapted to the conditions prevailing in each population has barely been studied so far. Fox (1936) and Fox and Wingfield (1937) demonstrated that individuals of a number of marine invertebrates taken from different latitudes have different respiration rates and differ also in the rate of heart beat and discovered that, as a general rule, respiration rate and other temperature-sensitive activities are the same in all populations, whatever the mean environmental temperature. Each population of a species proved to have a different temperature-activity relationship. At first sight this appears to be a case of genetic divergence and adaptation within each population, but there is now evidence that in some species at least, individuals transplanted from one population to another accommodate to the new environmental conditions, so that physiological differences may not always be genetically determined. Rao (1954) has demonstrated that a tidal rhythmicity in the rate of water propulsion by *Mytilus edulis* persists in the laboratory for long periods, but that when Atlantic specimens of this species are transplanted to the Pacific intertidal, the tidal rhythm changes from the Atlantic pattern to the Pacific within a week. Segal, Rao and James (1953) found that the rate of heart beat of *Acmaea scabra* and *A. limatula* and the rate of water propulsion of *Mytilus californianus* differed with the latitude in which the specimens lived and, in precisely the same way, with the height in the intertidal from which they were collected. The low intertidal and the sublittoral have lower mean temperatures than the upper part of the shore and are equivalent to habitats in higher latitudes. In all these cases, transplantation to a different habitat resulted, within a very few weeks, in a change in the rate of these phenomena to that found in specimens living naturally in that situation. Further examples of physiological accommodation will be found in the recent reviews by Bullock (1955) and Prosser (1955).

Phenotypic physiological differences between populations are not particularly

well known; phenotypic morphological differences are. They have not concerned the zoologist particularly, except in the taxonomy of corals, but botanical taxonomists have been aware of this problem for a long time, for the phenomenon is well marked in plants. In fact, a series of terms have been invented to designate and differentiate these phenomena: ecotypes, ecospecies, ecads, etc. (see e.g., Cain, 1944).

Phenotypic variation presents a problem of identification, though not of taxonomy unless it is decided, for some reason that phenotypes, ecotypes, etc., should be named and included within the taxonomic system. However, non-morphological genotypic variation presents a serious and fundamental problem, for the taxonomist has no suitable procedure for naming the new population. So few populations are known which exhibit physiological, but not morphological, differences, that no special taxonomic procedure has been devised yet. But with the rapid expansion of comparative physiology, ethology and, particularly of physiological ecology, this particular problem of nomenclature is likely to force itself upon the attention of systematists before long. Even though no data have been presented in this discussion which were not already well known to most taxonomists, very few have failed to ignore them as inconvenient facts, more or less on the principle that "if we do not look at them, perhaps they will go away." It is obvious that a taxonomic system based purely on morphology is indefensible. Type collections in museums are of very little value when one is concerned with species which can be separated from others only on physiological or behavioural grounds and the whole taxonomic procedure will need to be radically reorganised to accommodate them. With physiological and ethological species and subspecies, a new dimension has been added which, while not invalidating the whole of taxonomy, raises fundamental doubts about its validity as an exact science.

Of course, there is some doubt in the minds of many taxonomists whether it is worth naming all these physiological races and subspecies, accompanied by morphological characters or not. But it is one of the functions of systematics to name recognisably different groups of organisms and the problem is not changed if the differences can be recognised by a physiologist and not by a morphologist. It has been pointed out to me that in any species in which clines exist, it is common to find that a cline in one character is not coincident with a cline in another in the same species. Quite small populations therefore differ in some respect from neighbouring ones, and to name each population would result in a great multiplicity of subspecies and races, most of which could not be distinguished from each other morphologically at all. To name each population would reduce taxonomy to an absurd and impotent state, but unless this is done, the science is failing to achieve its nomenclatorial objectives. Systematists themselves appear to be undecided on the correct policy and there are two schools of thought. One tends to give subspecific or even specific status to any population which can be distinguished by some means from another. The second, of the opinion that taxonomy would only be confused by such a procedure, names as species only readily separable organisms and to a great extent disregards subdivisions of them.

The Indication of Relationship

When we consider the systematists' interest in the relationships between homogeneous groups of animals, the problems change, but are no less serious. It is not claimed that the present arrangement of organisms in supraspecific groups is perfect or settled. Revisions are constantly taking place as species are placed in new or different genera, families in new and different orders and so on. However, it is commonly urged by systematists that defects in the natural order of organisms,

which constitutes the present-day edifice of systematics, are due entirely to our lack of knowledge. It is argued that when more is known about the structure of organisms, their embryology, the fossil record, and when a greater number of plants and animals have been described, it will be possible to erect a final and perfect classification which will show precisely the relationships between all organisms. Ideally, presumably, were all the organisms that existed in the past, and all those that exist today placed before a systematist, he could devise a natural classification which would not only name each species, but would also group it with its relatives to show the evolutionary affinities of all members of the plant and animal kingdoms. This is a fallacious view and, in fact, the more that is known, the less it is possible to fit organisms into the Linnaean taxonomic system to show their phylogeny. Systematics, as we know it today, is possible only because of the fragmentary nature of our knowledge. Why else should it be that in the one group in which it is estimated that nearly all the existing forms are known and described, the birds, the Linnaean system should be faced with its greatest difficulties?

Systematics, as a science, is in a transitional phase, and in the last decade has advanced rapidly; but taxonomic procedure is conservative and has not advanced with the increased knowledge of the mechanisms of speciation. As a result taxonomy is based on an outmoded view of the nature of a species. So long as a species is regarded as a group of identical organisms which is sharply demarcated from any other group of organisms, current taxonomic procedure is adequate. But such a system is indefensible when it is conceded that intraspecific variation exists and that organisms are in the process of evolving. When to this is added the fact that the same systematic edifice is intended to include extinct as well as living organisms, the whole system is reduced to an absurd state. The contradictions inherent in modern taxonomy will be appreciated when it is recalled that descriptions of species are still based, at least theoretically, on descriptions of single type specimens which are then deposited in a museum. Fortunately, vertebrate zoologists, at least, have been forced to abandon this procedure and to base descriptions of species on series of specimens rather than a single type. Implicit in the whole technique of systematics is the eighteenth-century view that species are immutable and discontinuous, a view that was current when the Linnaean taxonomic system was devised. The entire science is thus committed to a view which no one seriously holds today.

The inadequacy of the present taxonomic procedure is evident in any field of systematics in which evolution of organisms is a factor to be considered—that is, in the study of infraspecific groups, in palaeontology, and in the taxonomy of any group of organisms with an excessively high reproductive rate, so that adaptation by evolution is rapid enough to be detected in a single population.

It is now obvious that in any widely distributed species there is a tendency for divergencies to become established in different parts of its range. This is particularly likely because the physical conditions in no two areas are identical, but even if they were, there is still some likelihood that divergence of isolated populations would take place. With few exceptions, the distribution of any organism is discontinuous and the degree of isolation of one population from the next depends upon a great variety of factors, including the mobility of the species, and the nature and extent of the intervening habitats. The minor differences which become established can be accommodated within the existing taxonomic system, theoretically at any rate, so long as the species is discontinuously distributed. The machinery exists for dealing with this situation although, if pressed to its logical conclusion, it would probably be impracticable to name each small population in

which differences from the main stock of the species have become established.

However, when a species is continuously distributed, or the discontinuities in distribution are slight, it is still possible for differences to become established in different parts of the range of a species. These may be of such magnitude that, were the species discontinuously distributed, the differences would warrant the erection of subspecies or even species. Such a situation often exists when clines are formed. This is particularly likely to occur when a species has a wide distribution, but its members do not move around appreciably, so that they tend to breed with other individuals in the same locality. There is the same likelihood of adaptation to local environmental conditions in each part of the range, although evolution is likely to be slower than when each population is isolated from the next. The clines may concern morphological features, correlated morphological and physiological features, or physiological features alone. Clines involving behaviour, such as differences in song of a species of bird—a possibility as yet practically unexplored—may also be established.

There is no means in the existing taxonomic system of identifying the part of a cline from which an organism was collected, nor is it easy to see any modification of the procedure which would permit such a designation to be made. It may be argued that it is not necessary to burden nomenclature further by including in the name of an organism the precise population from which it was collected. If this view is accepted, however, taxonomy is reduced to an extremely arbitrary and illogical state, for at present organisms which show a continuously graded series of differences over their geographical range are regarded as belonging to a single group, a group, moreover, which is by definition homogeneous. If the same organisms, showing the same differences over their range are discontinuously distributed, they may well qualify for elevation to subspecific rank. Leaving aside the question of non-morphological differentiation of populations, this means that the criteria for separating two specimens into their species or subspecies depends not only on the intrinsic differences between them, but also on extrinsic factors like the discontinuity of distribution. This at once disqualifies much museum taxonomy and especially the practice of describing a single type specimen of a species. It is really no solution to the problem to keep with the type, collections of the same species taken from different parts of its range, for it is one of the functions of systematics to name distinguishable organisms, and this is what it cannot do unless the populations of a species are isolated from one another and the differences between them well marked.

Something of the same problem occurs when two ends of a cline overlap to form a *rassenkreis*. The examples of the circumpolar Herring gull, *Larus argentatus* and of the Himalayan tits, *Parus major* and *P. minor,* are too well known to warrant further examination (Mayr, 1942; pp. 180, 182). Stebbins (1949) describes a perfect example of a *rassenkreis* in the salamanders of the genus *Ensatina* in California. He concludes that they have spread from an original centre of population in the redwood forests of northern California and southwestern Oregon, southwards along the coast ranges and east and south along the Cascade Mountains and the Sierra Nevada to meet again in the hills of southern California. The two arms of the chain are kept apart by the dry Central Valley. In southern California, *Ensatina* forms two sympatric species which differ considerably in appearance and do not interbreed. Stebbins' solution to the nomenclatorial problem posed by this situation is to regard the Californian salamanders of this genus as members of a single species, *Ensatina eschscholtzii,* and to name seven races or subspecies corresponding to the fairly distinct homogeneous populations in various parts of the *rassenkreis;* previously four species had been recognised. This leaves

unaccounted-for six regions where races overlap and interbreed. Since there is no recognised procedure for naming populations of a species which form a *rassenkreis*, this is inevitable. There is not even consistency in the status awarded to the end links of the chain which overlap and form sympatric species. In *Ensatina* they are regarded as members of the same species, in *Larus* and *Parus* as separate species.

Any taxonomic group, whether it be a subspecies, a family, or a class, is defined as being distinct and separate from any other. By and large they are distinct and separate and the taxonomic procedure is capable of accommodating them, but in cases where they are not, there is no mechanism for their inclusion in the system. In living organisms this difficulty is apparent only when continuously graded series of modifications in morphology exist, as in a cline, but in palaeontology there are not only geographical clines, but temporal clines also, and the problem is encountered much more frequently. It must be admitted that this problem is theoretical rather than practical at present because of the paucity of the fossil record, but this is no reason for ignoring it.

If continuous clines exist in response to gradual, but continuous changes in environmental conditions, it is equally true that a gradual change will occur in a single population of an organism in response to gradually changing ecological conditions over a period of time. If, as is usually the case, specimens of a particular population of fossil organism are known only from collections separated by great intervals of time, there will be sufficient differences between successive specimens in the series for each to be regarded as a separate species. This is equivalent to collecting specimens of a continuously distributed modern species at widely separated localities in its range and describing each as a separate species, or subspecies, ignoring the fact that they really form a cline and are not, therefore, to be regarded as separate. In the well-known orthogenetic evolution of the Equidae in the New World, it has been demonstrated by Simpson (1944) that only three changes in heterogonic growth rates of limbs and skull need be postulated to account for the entire evolution of the group. Most of the species and even genera which had been described are therefore arbitrary and artificial. Watson (1949) suggests that several other groups of mammals show similar orthogenetic evolution, where the same taxonomic problem must occur. If, as Crowson (1953) has proposed, not more than one major systematic character is evolving at any given time, the chances of gradual changes of this nature, with the taxonomic problems that they involve, must be greatly increased. This means that there is at least a strong probability that in the great majority of fossil series the ability of the taxonomist to separate species rests solely on the incomplete nature of the fossil record available to him.

Although the gradual shift in a single species may have been underestimated as a means of evolution, this is not to say that it is the only sort of evolution that has taken place, nor, indeed, that it is the most important. As Mayr (1942) and others have demonstrated, one common method of speciation may be the diverging of separate populations of a species, the later overlapping of the separate populations with competition between the two if they are sufficiently distinct, and the subsequent specialisation of each into separate habitats. On examination, allopatric speciation appears to be a continuous process, but with the addition of an extra dimension, space, to the original one of time. If speciation is always, or even often, a continuous process it is impossible to say where one species leaves off and another begins, and it follows that the species of the palaeontologists must often be fortunate accidents. As the fossil record becomes more completely known, the problems are not likely to be resolved therefore, as is generally supposed, but will become more acute.

It is not the purpose of the present paper to enter into the discussion of whether or not there is such a thing as "macroevolution," that is, the sudden appearance of new groups of organisms. There is a strong probability that the evolution of major groups is essentially the same as that of species, with the difference that at some periods the rate of evolution must be much higher than at others. This being so, there would be relatively few organisms of some intermediate form in comparison with the numbers of the stable, definitive form which remained more or less unchanged for long periods of time. With the fossil record as incomplete and poorly sampled at it is, it is not surprising that the intermediate forms should generally be missing from the collections of the palaeontologist. Thus there is a spurious impression of discontinuity, and supraspecific groups are created, although theoretically at least, no boundary can be drawn between them.

The problems which are theoretical rather than actual to the palaeontologist are real problems to biologists working with organisms which reproduce with great rapidity. For in these organisms, species evolve almost before the biologists' eyes and render the nomenclature of very doubtful value. The problem is most acute in the bacteria, though it is by no means restricted to them. In some areas where the insecticide has been in use, the housefly has developed great resistance to D. D. T. In one series of experiments with *Musca domestica,* successive generations of flies that survived exposure to D. D. T. were reared until a strain was developed that was 250 times as resistant as non-resistant strains. This selection required sixty generations in each of which 90 per cent of the flies were killed by exposure to D. D. T. (Annand, 1949). With such intense selection, any character with survival value spreads rapidly throughout the population. The result of this is that a population exposed to intense D. D. T. spraying for a number of years, as has happened in several parts of the world, evolves into a form with different physiological characteristics from the original form. Were both the original and the resistant strains living at the same time, they would be regarded as separate physiological races. The development of resistance to insecticides is an extreme example of the kind of changes which occur in every population of organisms exposed to changing selective pressures. The name *"Musca domestica"* was a short and convenient designation of an organism with certain morphological, physiological and behavioural characteristics. Since the extensive use of D. D. T. and other insecticides, the same name refers to an organism with slightly different characteristics. Not only has the organism for which *"Musca domestica"* was a symbol changed slightly, but the progress of the change has been continuous so that no boundary can be drawn between the old and the new *Musca domestica.*

The Language of Taxonomy

In all the cases examined, the difficulty is the same: that of using a nomenclature which tacitly assumes that species are immutable and discontinuous, whereas in fact they are neither. The difficulties inherent in the system will not be resolved by modifying taxonomic procedure in the descriptions of species by basing them on descriptions of series rather than on single type specimens, nor by devising better methods of describing clines, subspecies and physiological races within the existing system. These are temporary expedients and will give only temporary relief, for the difficulty is fundamental. It is only by accident that species can be observed as separate entities at all, because we can examine only those organisms alive today or else a few scattered fossils. We are somewhat in the position of examining a bush from one moderately complete cross-section, and a number of fragmentary ones. In such a view each twig appears

as a separate entity, quite distinct from the next one, and it is only occasionally that the cross-section passes through the junction between two twigs. This, of course, is well known and is accepted by all taxonomists, and yet the makeshift and pragmatical nomenclatorial system is expected to describe, accurately, the whole bush.

Viewed grossly, species which can be named do exist, in that there are periods of time, and places in space, in the history of a population of organisms where they are relatively stable and unchanging, and periods and places where they are undergoing rapid change. The relatively stable and unchanging state represents the species, and the brief transitory phase can be regarded as the boundary between two species—providing that one does not look too closely at it. This is perfectly adequate for most practical purposes, but it represents only a very rudimentary and unsatisfactory systematics. Viewed minutely, species are not discontinuous at all (except at the level of individual mutation), and logically, if a species is to be regarded as a group of organisms distinct from all others, divisions between species can only be made at the level at which discontinuities exist, and any group differing genetically in any respect from another should be regarded as a separate species. This would eventually involve naming each individual, clearly the *reductio ad absurdum* of systematics. Yet logically this is the position of nomenclature under the Linnaean system.

The problem is essentially one of language. Descriptions of species are verbal and words can only be used to describe discontinuous processes, since the words and the things they signify must be defined and to do that it is necessary to give them boundaries and limits. If, as is usually the case, there is no discontinuity between species, it is impossible to describe them precisely in words, though it is possible to give them an approximate description. Words are suitable for describing organisms at the level at which discontinuities occur, but as we have already observed, this involves a separate description of each individual organism. We are in the position of trying to describe a continuous mathematical curve verbally. This can be done only by describing each individual point on the curve, and there are an infinite number of them. The appropriate language for describing continuous and changing processes is that of mathematics where, theoretically, absolute precision is possible. This is the logical and obvious way of describing the evolutionary relationships between organisms and has been attempted in one or two simple cases (see e.g. Olson and Miller, 1951). There is no way of combining the nomenclatorial and systematic functions of taxonomy within a single system if precision is demanded. If names are needed for the use of non-systematists, they can be given to the relatively stable and unchanging parts of the curve, as they are today in what constitutes a "species," but this is not the way in which a sound and exact science of systematics can be developed.

Although it may be a logical proposal to suggest the use of mathematics to describe continuous processes (for which it is eminently suited), rather than words (which are eminently unsuitable), it is not a practical solution at present. The exact sciences have made enormous use of the mathematical tool and this has accounted for their great success, but even the simplest biological phenomena are vastly more complicated than any physical one. The attempt to describe the whole course of evolution in mathematical terms is beyond the capabilities of present-day biologists, mathematicians, and even of present-day mathematics, and will probably always remain so. However, the intention of the present paper is not to offer the solution to a problem and then to point out that the only solution is totally unattainable. Since it is evident that the language used in systematics is inappropriate and that the appropriate lan-

guage is beyond our capabilities, it is obvious that we should make the best use of the techniques at our disposal, and not ask the impossible of the science of systematics. In particular it is important that we should not forget that we are working with an inadequate tool and so not try to force organisms to conform with a view of the species concept which is coloured by a rigid taxonomy. In this context many of the disputes and discussions of systematists, such as whether or not species exist, whether or not it is permissible to create monogeneric families and, quite often, whether this borderline genus should be placed in this family or that, fall into their proper perspective. They are almost entirely due in the first place to the inadequacy of the whole nature of systematic procedure and in the second place to systematists' forgetting this fact. If we are unable to alter the system at present, these disputes are fruitless and irrelevant.

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Some Distribution Patterns of Pacific Island Faunae

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THIS paper concerns problems in the zoogeography of Pacific islands, based primarily on two families of insects, and notes comparisons with patterns in some other groups of animals. Some of the views here expressed are based on uncompleted research and are thus tentative.

The insects of Pacific islands are too insufficiently known for one to draw comprehensive conclusions on the basis of distribution, so only preliminary deductions can be made. The insect faunae of the various island groups are quite unequally known. For instance, those of Hawaii, Samoa, Marquesas, and New Caledonia are moderately to fairly well known, whereas those of Tonga, New Hebrides, and others have hardly been investigated. Extensive collections from Micronesia are now being studied at the Bishop Museum. Large collections from Fiji and Southeastern Polynesia, also at the Bishop Museum, have only been studied in small part. Furthermore, the rich source areas of the Solomons, New Guinea, and the Philippines, or regions to the westward, are imperfectly known. Among the studies of insect distribution made so far, widely conflicting views have been expressed.

Mayr (1941*a*, *b*) has given an excellent discussion of the distribution in Polynesia of birds, the best known group of animals, and has modified the outlines of the Polynesian Subregion. Mayr's outline differs from that accepted by most entomologists, and my early impression was that insect distribution would dictate conclusions other than those reached by Mayr. However, on analyzing distribution in the groups under study, my tentative outlines are not greatly different from Mayr's, as far as Polynesia is concerned. Further studies of insect distribution in the area will determine how correct Mayr may be in assuming that tropical land birds are as adequate indicators of insular zoogeography as are other groups of terrestrial animals.

In this discussion the following assumptions or facts are taken as basic to an understanding of the distribution of terrestrial organisms on Pacific islands, but space will not be taken for elaboration of each point. (See Mayr, 1941*b;* Usinger, 1941; Zimmerman, 1942, 1948; Baker, 1951; Gressitt, 1954.)

1. All outlying Pacific islands (except Galapagos, Juan Fernandez, New Zealand, and islands near New Zealand) belong to the Oriental Region and not to the Australian Region, although there is conspicuous New Zealand influence in New Caledonia, and New World and Holarctic influence in Hawaii.

The entire area (Fig. 1) may be termed the Polynesian Subregion, though more accurately it is a tapering fringe of the Papuan Subregion with overlapping influence from the Philippine Subregion and other areas. Within Polynesia, Hawaii and New Caledonia may each be assigned to a division of its own, and the rest to the division Polynesia proper, consisting of the subdivisions Micronesia (Bonin, Mariana, Caroline, Marshall, and Gilbert Islands), Eastern Melanesia (Santa Cruz, New Hebrides, and Fiji), Central Polynesia (Tonga, Samoa, Ellice, Phoenix Islands, etc.), and Southeastern Polynesia (Marquesas, Society, Tuamotu, Mangareva, Austral, Cook Islands; Rapa, and Easter Island). These subdivisions are not strict zoogeographical areas, but are

used more for convenience, and express, in part, degrees of impoverishment and, in part, different source areas. For instance, the boundaries between Gilbert and Ellice, Gilbert and Phoenix, and Phoenix and Fanning, are of minor significance, whereas between Fiji and Samoa, and Samoa and Society, greater contrasts exist.

2. There is a general tapering of quantitative representation (for islands of similar size) from west to east, particularly in relation to distance from continental areas.

3. There is also a qualitative tapering from west to east, rendering more isolated islands highly disharmonic in their faunae (fewer major categories represented). This is true even for larger or older islands with greater numbers of species than there are on intervening smaller or younger islands.

4. The extent of speciation on an island is directly related to the island's age, size, isolation, and diversity of environment. The degree of disharmony (scarcity of higher categories) and number of empty ecological niches are also of prime importance, as are climatic fluctuation, elevation and subsidence, eruptive cycles, and erosion cycles.

5. Atolls and other low coral islands have a small fauna—similar in widely separated groups of islands—which is limited by the lack of ecological diversity, the limited halophytic strand flora, the presence of brackish ground-water, the scarcity of soil, and exposure to salt-spray. High islands, on the other hand, can support much more harmonic faunae.

6. There is a general similarity in faunal composition on widely separated groups of islands. This is because they share to a greater or lesser extent a common source (Papuan-Philippine, with other lesser influences), and also because of the similarly selective means of transportation to the islands.

7. Certain types of animals are more likely to be dispersed across the sea than others are, and also more likely to establish themselves on oceanic islands (those islands not recently connected with continents and whose faunae could have arrived by dispersal over sea). In general, small insects and mollusks are dominant animals on most oceanic islands. Animals characteristically absent or scarce on oceanic islands are mammals (other than bats and rats), amphibians, land snakes, fresh-water insects, fresh-water fish, etc. Rats on all outer islands have probably been transported by man.

8. Animals are transported to oceanic islands by air currents (particularly in storms, or in currents circulating in directions opposite to vortices and to the general east-west trade winds, or in upper air currents), by floating logs or trees, or are carried on the feathers or feet of birds, or by man. (See Darlington, 1938; Zimmerman, 1942, 1948; Gressitt, 1954, for several of the preceding points.)

9. Evolution may be rapid on isolated islands characterized by empty ecological niches, an absence of predators and competitors, and a lack of gene-intermixture from parent populations; but long periods of time are necessary for an accumulation of colonists to pass successfully the obstacles of the "sweepstakes" route (Simpson, 1953) and reach such islands. Chances of survival are related to an inverse power of the distance, size of island (1/500 of the Pacific is land), and difficult physiological (as well as other) obstacles. Species that have evolved on old isolated islands appear to be subject to ready extermination under changing ecological conditions. This tendency has been explained on the basis of a depletion of their genic variability; however, this idea does not conform to the current thought of some geneticists. Some of these factors are not fully clarified. Oceanic insects are for the most part small and sedentary, and are generally represented by small populations with restricted distribution. They often appear to represent relicts, but the genetic explanation of relicts is still unsatisfactory. Yamashina (1953) attempted to show that populations on smaller islands produced new

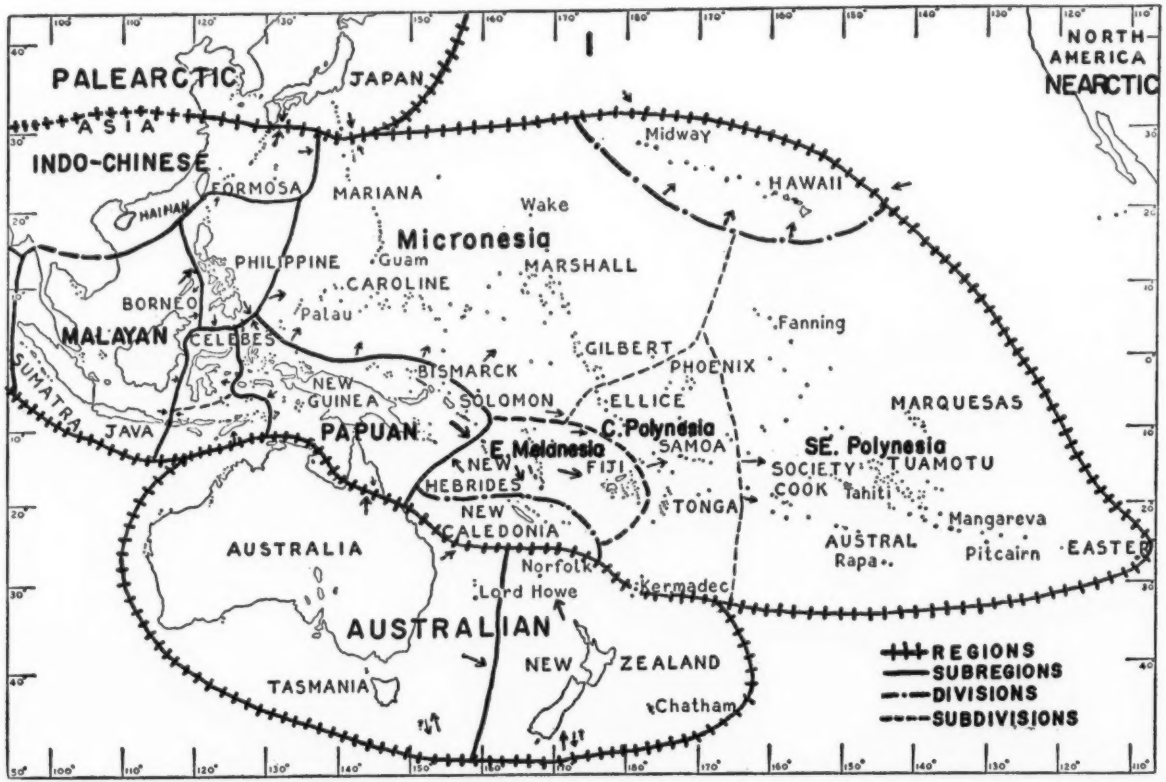

FIG. 1. An attempt at a faunal subdivision of the Pacific area. Portions of the Palearctic and Nearctic, and all of the Australian Region are included, but the greater part of the map is concerned with subdivisions of the eastern part of the Oriental Region. The Indo-Chinese, Malayan, Philippine, and Papuan Subregions of the Oriental are indicated. The Celebes area (old Wallacea) is a heterogeneous transition area of less than subregion rank, and the subdivisions indicated are rather arbitrary. Weber's Line, separating this area from the Moluccas, is in part of less value than the border of a subregion. The remaining areas combined may be called the Polynesian Subregion, but constitute a fringing area of gradually diminishing representation. The fauna of this Subregion is admixed with those of the other subregions and regions shown on the map, especially with that of the Papuan, and, in its western part with those of both the Philippine and Papuan Subregions. Micronesia, Central Polynesia, Southeastern Polynesia, and Eastern Melanesia together comprise the division which can be called Polynesia proper (of equal value with Hawaii and New Caledonia), with the first three of much lesser value than Eastern Melanesia. Arrows indicate probable directions of faunal interchange in later periods of geologic time. Size of arrows suggests relative importance of influence.

genera more rapidly than those on larger islands.

10. The general conformation of the Pacific Basin is of a relatively permanent nature, and probably few relatively major changes of land and ocean bottom have taken place. There have been some changes of sea-level (elevation or subsidence), development and erosion of volcanoes, and growth of coral. The mid-Pacific continents and numerous landbridges of some earlier zoologists have already been dispensed with by Mayr (1941*a*), Usinger (1941), Zimmerman (1942, 1948), and others. However, there have apparently been more high islands in the central Pacific in the past than there are at present (see below).

11. Not all islands with continental rocks are necessarily continental in fauna. To a zoologist, continental islands are those that have been connected to a continental area in relatively recent times, say, since the Mesozoic, and have since remained above water. Thus they do not require over-sea dispersal to explain their fauna.

Oceanic or Continental?

Mayr (1941*a*, *b*), in discussing the distribution of birds, claims that Fiji, New Hebrides, and New Caledonia are oceanic islands, in addition to Polynesia and Micronesia. Entomologists have rather consistently called them continental, and some have even called Tonga, Samoa, Palau, and Yap, continental (Esaki, 1950, and others). The faunae of Fiji, New Hebrides, and New Caledonia are much richer than those of the other island groups; they include many insects of large size, more groups appear to be represented in them, and they have developed many endemic genera. However, a comparison of subfamilial and tribal representation in the Cerambycidae (longicorn beetles) and Chrysomelidae (leaf beetles) indicates that Fiji has only one more subfamily of Cerambycidae than does Micronesia or Samoa, and only one less subfamily in the Chrysomelidae than does Samoa. New Guinea has at least twice as many subfamilies of Chrysomelidae as Fiji (which has six), and in addition there are two subfamilies known from the Philippines which may also occur in New Guinea. Fiji has more tribes of Cerambycidae than Samoa has, but fewer than Micronesia; Fiji has a few more tribes of Chrysomelidae than either Micronesia or Samoa. New Guinea has about three times as many tribes of Cerambycidae as Fiji, and about six times as many genera. Furthermore, the Fiji fauna for these groups is better known than is that of New Guinea. More of Fiji's genera of Cerambycidae are apparently endemic than is the case for either Micronesia or Samoa. This, however, is not true for the Chrysomelidae. It is undeniable that these islands are within the Sial, or Andesite, Line, but so are the Bonin and Mariana Islands, which are obviously oceanic in fauna.

New Caledonia has a high proportion of endemic genera, but a total of less than one-half as many tribes of Cerambycidae and less than one-quarter as many genera as New Guinea, even though its fauna is probably better known than that of New Guinea. An additional factor in the case of New Caledonia is that its rocks are largely serpentine, soil from which supports a most primitive and peculiar flora. This flora undoubtedly restricts the types of insects that could establish there. These cerambycid beetles of New Caledonia have clear relationships with those of New Zealand as well as those of New Guinea, but rather little with those of Australia, despite this continent's proximity. New Caledonia is less clearly oceanic, and less clearly Polynesian, than are the New Hebrides, Fiji, and the rest of Polynesia. The Loyalty Islands apparently fall into the same category as New Caledonia. The insects of New Hebrides are little known. New Hebrides appears to be oceanic with a poor fauna as compared with that of the Solomons, and it has far fewer endemic genera than has either New Caledonia or Fiji. The Santa Cruz Islands are entomo-

logically more related to New Hebrides than to the Solomons (R. A. Lever, personal communication).

Frogs (Fig. 2) are present in Palau and Fiji, but they are of types whose larvae do not require abundant water. Their presence should not be taken as proof of the continental origin of these islands (Myers, 1953*a*). The Palau species, *Platymantis pelewensis,* lays its eggs on grassy ground, and the larva metamorphoses in three weeks, living entirely on the yolk. There are no gills, and respiration is aided by a great expansion of the abdominal skin (Atoda, 1950). The two or more Fiji species belong to *Platymantis* and *Cornufer* and appear to be endemic (Brown and Myers, 1949). Inger (1954) unites *Platymantis* with *Cornufer.* Several kinds of snakes also occur in Palau and Fiji, but raft dispersal should not be ruled out.

Fiji, New Hebrides, and New Caledonia, as well as Palau, do not possess mammals other than bats and rodents, and in this respect also are oceanic. Palau, in spite of having a more harmonic fauna than the other parts of Micronesia, has conspicuous gaps including insect groups well represented in the Philippine-Papuan area. If any of these island groups had continental connections in the Tertiary and were not since submerged, insects of many more higher categories should be represented. Many unexploited ecological niches can be observed. The normal low population densities and the cryptic nature of the fauna of oceanic islands are characteristics also evident on these islands.

Contrary to the situation on many oceanic islands, some quite large insects do occur here, particularly in Fiji. Among these are very large stick insects and one of the largest beetles in the world. The latter is a prionid like the largest beetles in Micronesia and Samoa. These develop in dead wood and, like many weevils, are heavily sclerotized, and tenacious of life. Moderately large stick insects are fairly well represented on many oceanic islands, such as the Marianas, Carolines, Marshalls, and Samoa. They could have traveled on floating trees, or in palm-frond baskets holding food provisions in early sailing canoes. Stick insects also have well-protected eggs.

Distribution Patterns

Certain patterns are evident from a preliminary analysis of the distribution of certain families of insects among Pacific island groups. A few groups are found on almost every island with endemic species on the high islands. Many of the genera, including some endemic to Polynesia, are of wide distribution. Other groups are of sporadic occurrence, or are found on the island groups less distant from the Papuan Subregion. Some insects associated with strand vegetation are widespread on coral islands and the shores of high islands.

Drawing outlines of the distribution limits of certain groups (Fig. 2), one finds that the weevils are the most widespread group, being found on nearly all islands. They have speciated extensively and are often flightless. Weevils are perhaps the toughest of insects, and thus most likely to survive over-sea dispersal. Most of them feed in dead wood, twigs, seeds, or leaves, any of which could be carried through the air, or float, to islands. Zimmerman has studied the speciation of certain weevil genera on Rapa (1938) and other islands in Southeastern Polynesia (see also Van Dyke, 1937). When the Pacific weevils have been more thoroughly studied, a better picture of Polynesian zoogeography should develop. The ciid and anobiid beetles are also widely distributed. The beetle family Proterhinidae, formerly thought to be endemic to part of eastern Polynesia (Buxton, 1935), has been united with the Aglycideridae. The latter, though absent on the major continents, occurs in New Zealand and some Atlantic islands. A species was recently taken on Kusaie Island, extending the family's range to Micronesia.

Some small moths (Microlepidoptera) are also represented even on outlying is-

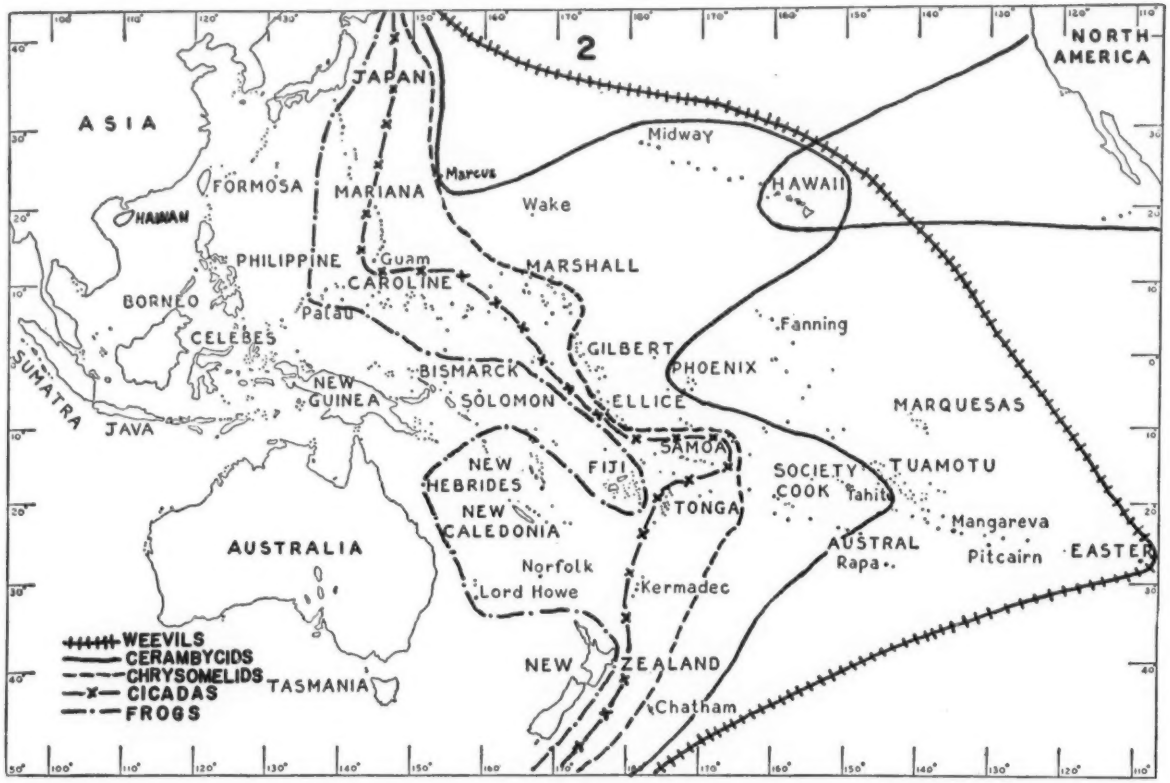

FIG. 2. The limits of distribution in Polynesia of five groups of animals representing different abilities for over-sea dispersal. The two lines for cerambycids indicate that parent sources were both Oriental and American.

lands. Unfortunately, land-bridges were invoked to explain their distribution (Meyrick, 1926), whereas such bridges would have brought many other groups which have never occurred on the islands. Furthermore, many of these small moths develop as miners in leaves, as borers in twigs or seeds, or as denizens of bark or debris, all of which could be carried through the air.

Land snails are well represented in Polynesia. Contrary to the situation in insects, three (or four) of the fifteen (sixteen) families (*sensu lato*) of Polynesian land mollusks appear to be endemic. According to Kondo (personal communication) the Tornatellidae (Achatinellidae) are well developed in Hawaii, the Austral-Rapa-Mangareva area, and Juan Fernandez, and also occur in the Bonin, Mariana, Caroline, Society, and Kermadec Islands. A few species are more widely distributed, and one even occurs on Mauritius. The Partulidae occur on most oceanic high islands except Hawaii, Truk, Juan Fernandez, and the Bonin Islands. The existence of Partulidae also in the New Hebrides, Solomon, Bismarck, and Admiralty Islands suggests an Indo-Malayan origin, but there may be a remote South American and Asiatic relationship through Antarctica. The Amastridae are endemic to Hawaii, having evolved from the widespread Cochlicopidae through one or two chance migrants (waifs). The Zonitidae, non-endemic and widespread, are largely derived from southeast Asia, but with a part derived from the Holarctic (supposedly transported by birds), while a third section is endemic to Polynesia. The supposedly endemic families are all primitive and low in the scale of Pulmonata, according to Kondo. They may be relicts whose continental ancestors have disappeared through their failure to meet competition with higher forms, as suggested below for certain beetles.

The Cerambycidae represent a slightly less extensive distribution pattern, with endemic species apparently absent on many outlying groups or low islands, such as the leeward Hawaiian Islands, Marcus, Johnston, the Phoenix and Line Islands, Christmas Island, the Marquesas, Tuamotu, Mangareva, Austral, and Cook Islands, Rapa, and Easter Island. The family is represented on some of these islands or island-groups, but only by widespread Polynesian species, which may in part have spread from Samoa and Tonga, or perhaps for the most part were spread from these sources via Tahiti by the migrations of the Polynesians. A few species are of wide Oriental distribution, and a few, particularly in the Marquesas, have been recently introduced from the New World. On further study, the representatives of the Polynesian genera which occur on a few of these outlying island groups may prove to be endemic forms.

In Hawaii the Cerambycidae are represented by about a hundred endemic forms (apparently descended from only three original colonists) as well as by widespread forms introduced by man. Of the three ancestral native strains, two are primitive nocturnal forms feeding in dead trunks; each of these is still represented by a single endemic species typical of the ancestral genus. One is Oriental, the other nearly cosmopolitan. The third line is more advanced (of diurnal habit), and has speciated into about a hundred kinds, which have been assigned to six closely knit genera. Many of these attack living plants, exhibit extreme host-specificity, and are limited in distribution. Some of the known species are already extinct, and some lowland species probably never were collected. This situation is somewhat similar to that in the native Hawaiian birds, which boast the endemic family Drepanidae; these birds, however, are probably of American origin, whereas most groups of Hawaiian animals are of Oriental (and a few of Australian) derivation.

In Micronesia (Gressitt, 1956) 88 percent of the 100 indigenous cerambycids are endemic. They belong to 34 genera, only five of which are endemic. Two of the endemic genera, one in the Bonins

and one in Palau, are flightless. Two other endemic groups show a tendency towards reduction of wings. One minute species among these has developed the faculty of jumping. The relationship of 16 percent of this group is Oriental, 12 percent Oriental-Papuan, 14 percent Philippine-Papuan, and 58 percent Papuan-Oceanic (including some Malagasy relationships discussed below). The Bonins possess some southern Japanese or Ryukyuan forms of Oriental genera, but these islands are clearly Polynesian (Micronesian). The Mariana and Palau Islands possess a higher proportion of Philippine elements than does the rest of Micronesia, although Palau is also strong in its Papuan relationship. Palau is the richest group in Micronesia.

Twenty-three of the 35 Samoan species of Cerambycidae are endemic, and the rest are held in common with Tonga or Fiji. Their relationships are 30 percent Central Polynesian, 15 percent Micronesian, 10 percent Fijian, and 45 percent Papuan-Oceanic. Eight of the nine nonendemic genera, including some thought earlier to be endemic, occur also in Micronesia. Three genera appear to be endemic. In Fiji 105 of the 112 species are endemic, and 18 of the 42 genera are endemic, with relationships dominantly Papuan, or Papuan-Oceanic. Tonga and the Society Islands possess only a few known endemics.

The longicorns from Micronesia, Central Polynesia, and Fiji, discussed above, belong largely to groups of nocturnal habit which bore in dead twigs, branches, or trunks. This suggests that they might have reached the islands in storm-blown twigs or floating logs, or might as adults have been carried in air currents. Being nocturnal, they would be more likely to be on the wing in bad weather. Some large tribes or genera of conspicuous diurnal cerambycids, well represented in the Philippine-Papuan area, are completely absent in all of Polynesia. Since many of these bore in living trees as larvae and are active and sun-loving as adults, they are unlikely to be on the wing in bad weather, or successfully to immigrate on log rafts. In general, the situation in this family seems to be similar to that in birds, as outlined by Mayr (1941*a*, *b*), although there appear to be no endemics on some outlying groups. The New Caledonian picture, however, is rather different, in that there appear to be almost no close ties with Australia, but rather a high generic endemism with both New Zealand and Papuan relationships. The New Caledonia-New Zealand relationships are largely in a tribe (Enicodini) limited to the two island-groups, but of principally Papuan rather than Australian affinity (Fig. 5). Many families of insects appear to have distribution patterns in Polynesia which are similar to that of the Cerambycidae.

The closely related beetle family Chrysomelidae (Gressitt, 1955), however, has a more restricted pattern. Although on the continents this family has more species than does the Cerambycidae, it is less well represented on oceanic islands. This relatively poorer representation is possibly due to the fact that these leaf-beetles are less sclerotized, shorter-lived, and diurnal, and require more food in the adult stage; furthermore, many have larvae which live in more exposed situations (on leaves, or on roots) and are thus in danger from salt-spray or brackish ground water. Of the 30 species thought to be indigenous to Micronesia, 26 are endemic; two (in the Bonins) may be of southern Palearctic or Indo-Chinese origin, and the rest are Philippine-Papuan or Papuan-Oceanic. Six live in the crowns of large monocots, both as larvae and as adults; three are casebearers as larvae, and at least one is a leaf-miner. Those with root-feeding larvae are found only on high islands and only in Western Micronesia. Only one occurs in the Marshalls; this is the coconut hispid, occurring also on Kusaie and Ponape.

Chrysomelidae are absent from the native Hawaiian fauna, and also from the Marquesas and Society Islands and all of eastern Polynesia. In Samoa, 13 of the 17 species are endemic, and two genera

appear to be endemic. The relationships are Papuan-Fijian, having less in common with Micronesia than in the case of the Cerambycidae. The fauna of Fiji includes 45 endemic species out of 60, and these exhibit Papuan-Asiatic affinity. There is only one endemic genus in Fiji. Many of the Fijian and New Caledonian species belong to the subfamily Eumolpinae, which is moderately represented in Samoa and Micronesia.

An example of a still more restricted distribution in Polynesia is the Cicadidae (Fig. 2), with about seven species each in the Carolines and Fiji, three species in Samoa, and two in the Bonins. This roughly parallels the distribution of the best-represented thoroughly aquatic order of insects, the Trichoptera, which has one species in the southern Mariana Islands, one to three on each high group of the Carolines (three in Yap), one in Samoa, and perhaps ten in Fiji. Cicada nymphs are root-feeders, a habit that limits their dispersal and survival ability.

Of the most restricted occurrence, perhaps, are the frogs (Fig. 2) in Palau and Fiji, the four land snakes in Palau and eight in Fiji, the single mayfly in Yap and the one in Samoa. Scarab beetles, with their soil-inhabiting grubs, are found only in Palau and a few other islands, though some introduced species are quite successful on high islands. The hardier freshwater insects such as beetles and true bugs are widespread, particularly the beetles, which have a few representatives in Hawaii, the Marquesas, and the Society Islands. The marine waterstriders are widespread, but have local endemic species.

Other groups poorly represented by endemics are the Embioptera (delicate bark-dwellers), Anoplura and Siphonaptera (associated with mammals), Strepsiptera (complicated host relationships), butterflies (sensitive larvae, fragile wings), and other fragile insects. Groups totally absent include the Plecoptera, Megaloptera (aquatic), Mecoptera (delicate), and Hymenoptera-Symphyta (exposed leaf-feeders); but these are also in part predominantly temperate.

Among several insect families represented in Polynesia, direct relationships with the Malagasy Subregion have been noted. Several of these involve closely related species in Micronesia and central Polynesia and in the Seychelles, Mascarene Islands (particularly Mauritius), or even Madagascar (Figs. 3, 4, 7, 8). In some of these cases [including *Glaucytes* (Gressitt, 1953), *Longipalpus, Prosoplus, Brontispa,* and other beetle genera the taxonomy of which is not yet published] the genera are not known from continental Asia, or even from New Guinea. The latter, or most of them, may represent survival of primitive forms on oceanic islands or elsewhere with restricted competition from advanced forms. Alternatively, some may represent inter-island waif dispersal of forms that could not establish themselves on continental Asia. Since the fauna of India is fairly well known, these patterns are puzzling, though a few of the genera involved are represented in Ceylon. Wider studies must be made, and New Guinea better investigated, before conclusions are drawn. On the other hand, some Micronesian relationships with India which seem to skip the Philippine and Papuan Subregions are also appearing.

Recent Geological History

Thus far, no clear evidence has been found in Micronesia of remnants of a fauna of former islands in the central Pacific which might have served as "stepping-stones" for the Hawaiian fauna of Oriental-Papuan derivation. It has become evident that in spite of the improbability of a former mid-Pacific continent, there has been considerable sinking in the central Pacific for some time (Mayr, 1953*a*). Two more recent discoveries throw further light on the problem. Both suggest that the ocean floor has sunk at least 1500 meters in the area of the Marshall Islands and to the east, south of Hawaii. Surface-living Creta-

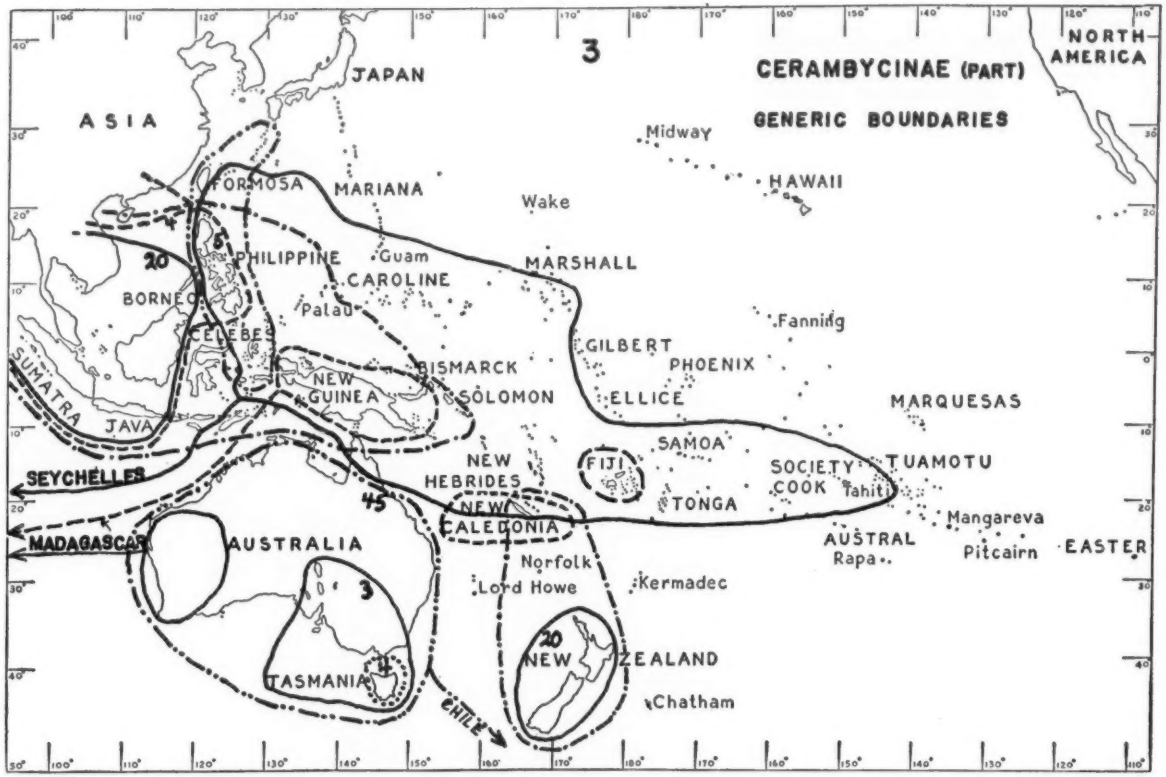

FIG. 3. Generic boundaries in some of the more primitive tribes of the subfamily Cerambycinae, family Cerambycidae. Each line represents the range of a single genus, except where figures are given. Asian genera not reaching Wallace's Line are omitted. Further data presented in Figure 4.

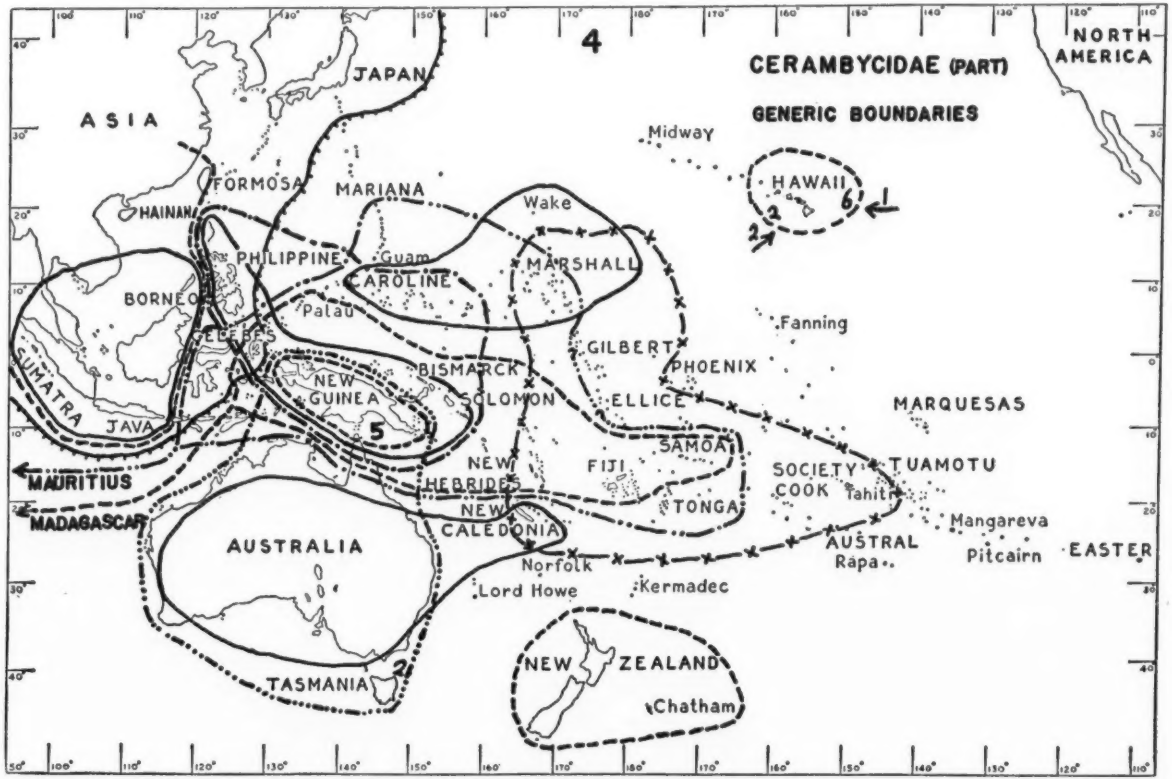

FIG. 4. Generic boundaries in Cerambycidae. The ranges of twelve genera in outer Polynesia, including all eight genera native to Hawaii. Each line represents the range of a single genus, except where figures are given. Arrows for Hawaii indicate source of origin, with numbers by arrows indicating number of genera of original immigrants.

ceous Foraminifera have been found on guyots (flat-topped sea mounts) below this depth (Hamilton, 1953). The borings in the Marshalls, at Bikini, and particularly the 1952 drillings at Eniwetok Atoll (Ladd *et al.*, 1953) have for the first time proved the existence of a volcanic foundation of an atoll, as hypothesized by Darwin. The evidence indicates that the latter atoll developed around a sinking volcano which was once above water. Although erosion may have first reduced the volcano to sea level, as is demonstrated in various stages in the leeward Hawaiian Islands, much gradual subsidence has also taken place. The two drillings first reached basalt underlying the coral, at about 1300–1400 meters below sea level, which is nearly 100 times the depth to which coral grows. Apparently the island started to subside in the Eocene; this might make it too old to have served as a direct stepping-stone, though its fauna might have been passed on to other high islands which later disappeared. At any rate, the present atolls could hardly support many remnants of a high-island fauna.

The insects of the Marshall Islands are largely forms of wide distribution although, interestingly, a few apparently endemic species of Polynesian or Oceanic (Malagasy to Polynesia) genera have been found. The nearby high islands, Kusaie and Ponape, do not appear to have many old relicts, and their fauna is younger than that of Hawaii, with few endemic genera. The eastern Carolines have many faunal elements in common with Samoa and Fiji, and these are probably forms capable of over-sea transport from Papua. When comparing the assemblage of these phytophagous beetles in the eastern Carolines with that of Hawaii, it is seen that the eastern Carolines have endemic species in more genera of Cerambycidae than Hawaii does, even though the total number of endemic species is far smaller. The eastern Carolines have endemic species in four genera of Chrysomelidae, but the family is absent from Hawaii. This correlates with geological evidence for the younger nature of the eastern Carolines, and also with their lesser degree of isolation. If Hawaii had many large "stepping-stones" in the mid-Pacific at the proper times, it might have a more harmonic fauna. However, the Hawaiian Islands may be older than indicated by Zimmerman (1948). There are many Hawaiian-Marquesan relationships (Adamson, 1939).

Sources of Polynesian Fauna

For sources of the Polynesian insect fauna the general Papuan-Philippine area is clearly indicated. Despite the facts that the insects of this rich fauna are too inadequately known, and that the relations of this area to Australia and the Malayan Subregion are insufficiently known, there nevertheless appear certain rather striking indications of strong differences and relationships. Examples will be given from the groups that I have studied, which present a picture somewhat different from the evidence from bird distribution (Mayr, 1944, 1953*b*), but which agree in part with proposals made by some botanists and entomologists (Dickerson, Merrill, *et al.*, 1928; Karny, 1929; Lam, 1934; Scrivenor, *et al.*, 1943; Lieftinck, 1949, 1953).

Primarily on the basis of geographical boundaries of genera in the two families of beetles discussed above, the following tentative points seem indicated. New Guinea has a rich fauna which has had wide influence in Polynesia, and is also felt as far northwest as the Philippines, as far west as Celebes, as far south as northern Queensland, and less directly, to (or possibly from) New Zealand, through New Caledonia. The influence of South America—through Antarctica and New Zealand stepping-stones—may have extended as far as New Guinea, or farther. The northern boundary of the Australian region is just north of Australia, except that the Cape York Peninsula of northern Queensland is excluded and is considered with New Guinea as part of the Papuan

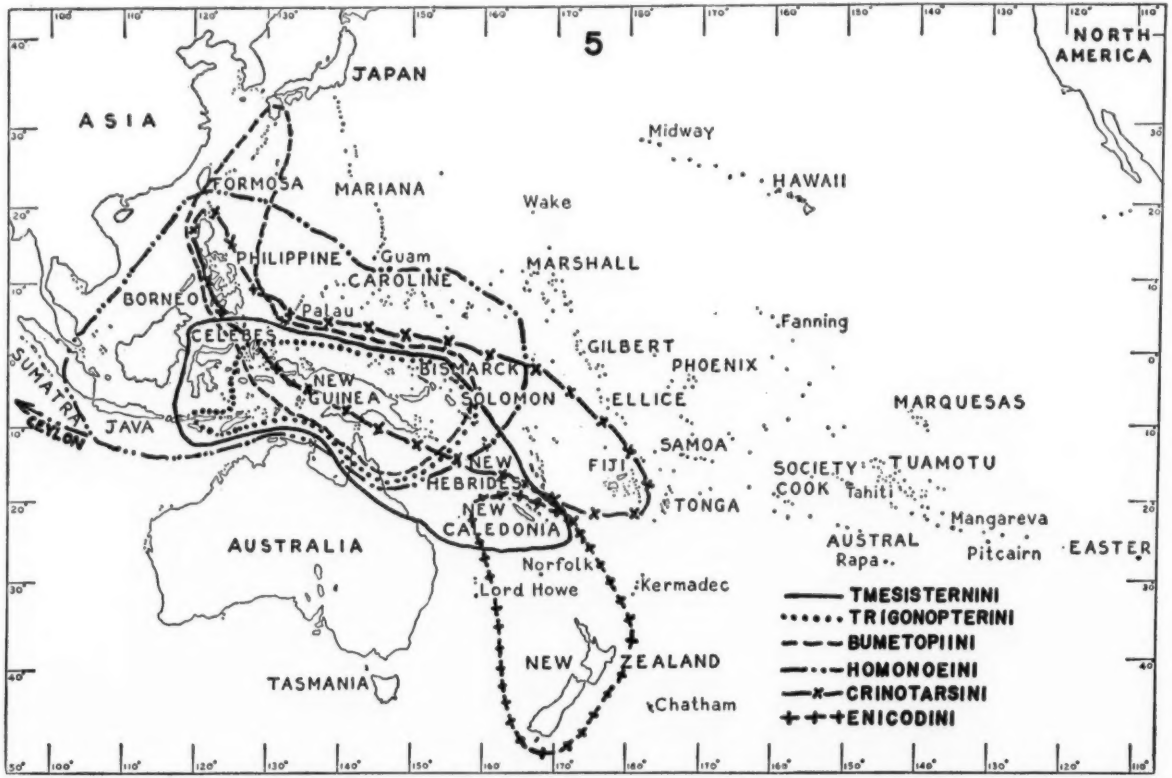

FIG. 5. Outlines of the distribution of the six tribes of the very distinct Tmesisternini tribal complex (Cerambycidae: Lamiinae), which has several hundred species. Only a very few of these occur west of Celebes or north of the Philippines, and the group has no clear outside affinities except in New Zealand.

Subregion of the Oriental Region. The Australian Region includes New Zealand as an extremely strong subregion which has had long isolation and some ancient (or over-sea) interchange with Papua and also with Antarctica and Chile, although Simpson (1940) has questioned such interchange. New Guinea is in part extremely old, with rocks in the north said never to have been submerged since pre-Cambrian time (Cheesman, 1951), although other views have been expressed (Lam, 1934; Mayr, 1953*b*). It may have had early Mesozoic connections with Asia, which gave it an Oriental fauna essentially different from that of Australia, at a period when New Guinea and Australia were well isolated. Miocene-Pliocene tectonic movements raised New Guinea until it was connected with the Cape York Peninsula, allowing an interchange. Australian elements among these beetles, as among the marsupials, went as far as Celebes, but are principally limited to New Guinea, particularly to the less humid southern part. New Guinea elements went as far as the Cape York Peninsula and there were halted by climatic barriers or other barriers perpetuated by climatic barriers.

Thus, at the time when New Guinea was temporarily united with Australia (as has probably happened more than once subsequently, during the Pleistocene sea-level fluctuations), New Guinea had already been long separated from Asia by a wider gap than at present (possibly between Weber's and Wallace's Lines). This prevented most Asian mammals from penetrating the intervening younger area —often called Wallacea (Celebes, Lesser Sunda Islands)—and the Papuan Subregion. At the same time, marsupials were prevented from reaching Asia. The New Guinea mammals include only bats, rodents, marsupials, and a monotreme (Tate, 1951), a fact that points to Australian relationship. The birds also show more Australian than Asian relationship (Mayr, 1953*b*), contrary to the situation in various groups of beetles.

During part of the mid-Tertiary, New Guinea and the Philippines may have had closer stepping-stones, permitting more interchange, at a time when the Philippines were more isolated from Borneo. This resulted in New Guinea and the Philippines having many elements in common which are not found west of the Philippines. On the other hand, some of the elements in the Philippines and New Guinea that are not found west of Celebes and the Philippines may represent primitive forms which have been pushed eastward from southeastern Asia and become extinct from inability to meet competition west of the line. This would be similar to the case of some Amphibia, as has been determined by Inger (1954). Insect distribution suggests that the presence of fresh-water fish in Mindanao might be attributed to human agency, or at least some factor other than a recent Borneo-Sulu-Mindanao land-bridge as suggested by Myers (1953*b*). According to Myers (1953*a*), Luzon has never been connected with Sundaland, and New Guinea and Australia never connected with Asia, at least since the Paleozoic.

Examples of distribution patterns of genera of the more primitive tribes of the subfamily Cerambycinae (Phoracanthini, Cerambycini, and others) are shown in Figures 3 and 4, with the addition in Figure 4 of a few samples of other patterns in other groups of Cerambycidae in eastern Polynesia. The former groups are extensively developed in the Australian Region and have relationships with the Neotropical fauna. Strong demarcation of ranges along the eastern border of the Malayan Subregion and along the northern border of the Australian Region are quite evident. The relative poverty of Celebes and the Lesser Sunda Islands is demonstrated, as is the possession of common elements by the Philippines, Moluccas, and New Guinea, or these in addition to parts of Polynesia. Four genera are common to areas east of the modified Wallace's Line and to the Seychelles, Mascarenes, or Madagascar, and another is common to Australia and Madagascar,

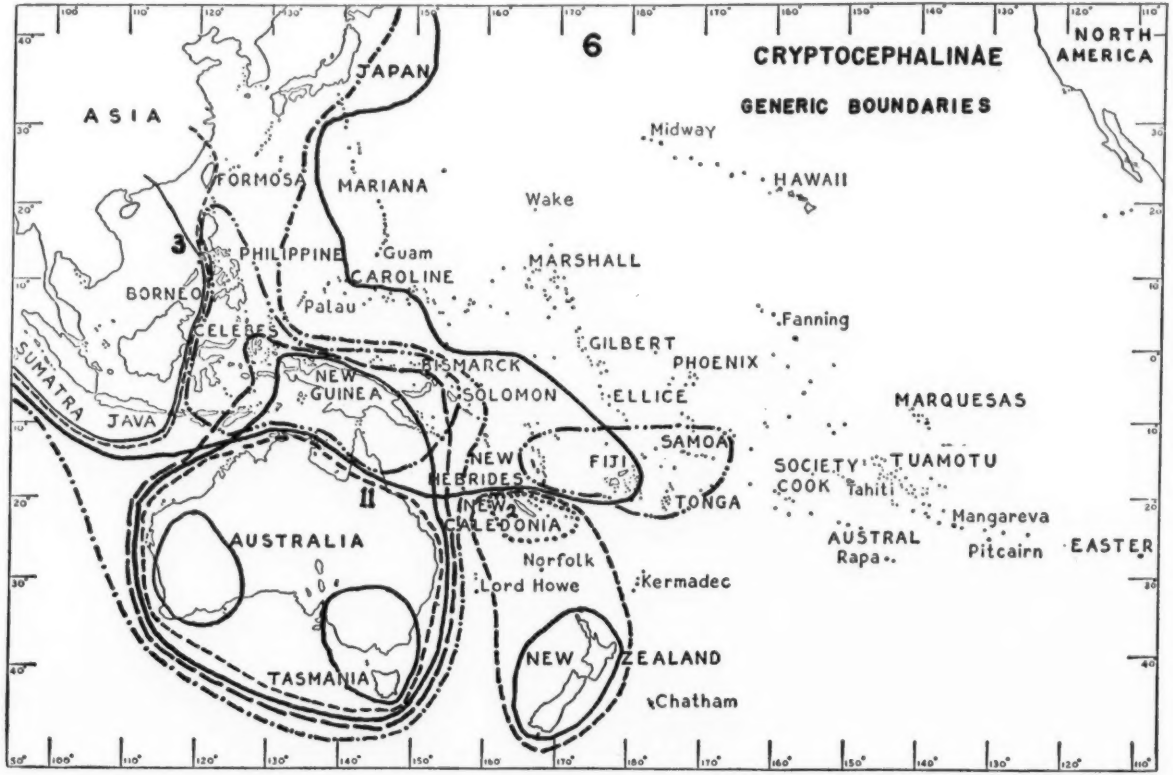

FIG. 6. Generic boundaries of the subfamily Cryptocephalinae, Family Chrysomelidae. Each line represents the range of a single genus, except for three genera limited on the east by the modified Wallace's Line. Two genera are limited to New Caledonia, and eleven to Australia proper (exclusive of North Queensland) besides two with more limited distribution in Australia. Asian genera not reaching Wallace's Line are not shown.

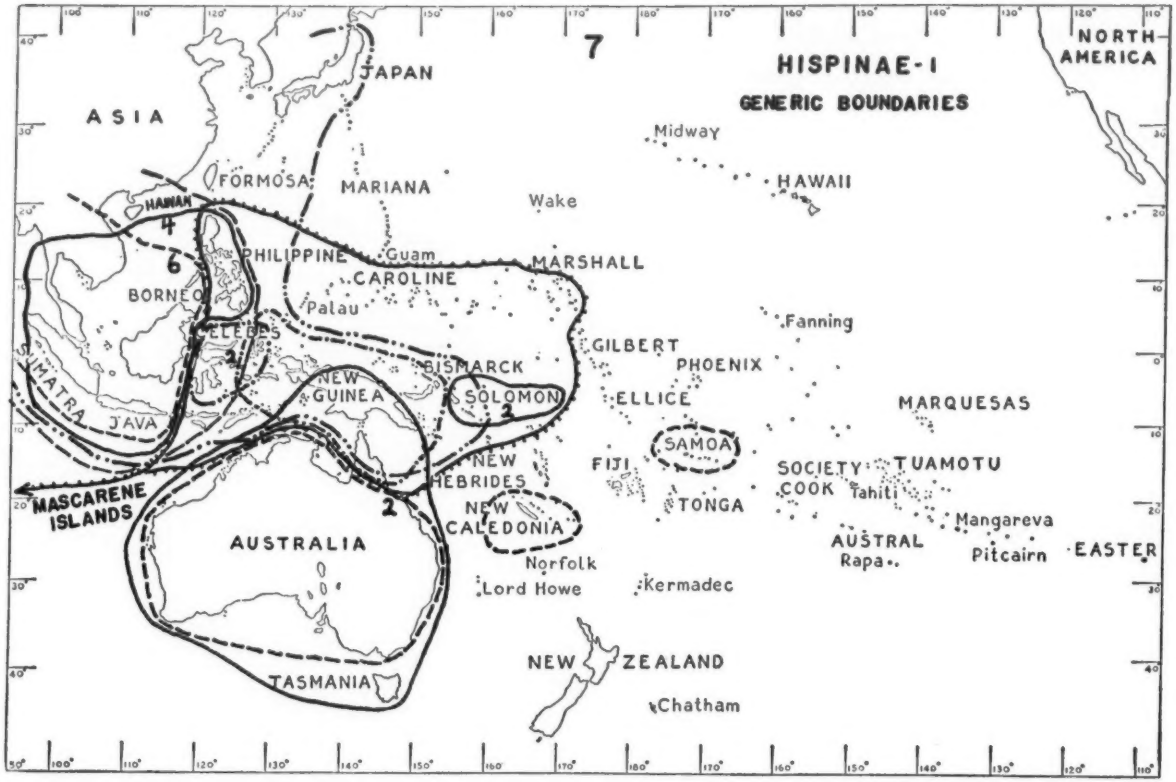

FIG. 7. Generic boundaries for a part of the subfamily Hispinae, Chrysomelidae. Further data for subfamily in Figure 8. Each line represents the range of a single genus, except that six genera are not found east of the Sunda Islands or Palawan, four are common to the Sunda Islands and the Philippines, two are restricted to Celebes and the Moluccas, two to the Solomons, and two to Australia exclusive of Cape York Peninsula, besides one common to Australia and New Guinea.

tralia and New Guinea.

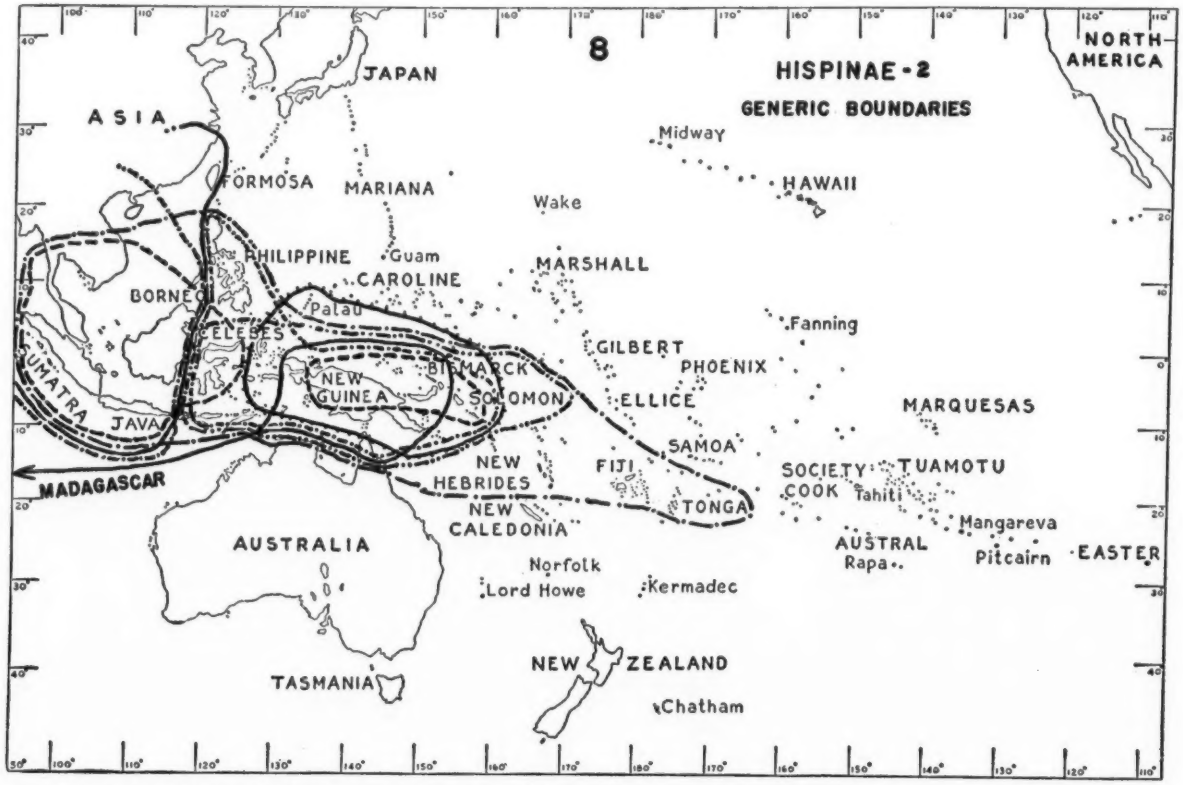

FIG. 8. Generic boundaries in the rest of the subfamily Hispinae, Chrysomelidae (see also Fig. 7). Each line represents the range of a single genus. Asian genera not reaching Wallace's Line are omitted.

Australia possesses 56 genera, and New Guinea 12, but only two are common to both. The situation in these groups approaches that in the gryllacridids, in which Karny (1929) stated that, with the exception of one group, the relationships between Australia and South America were closer than those between Australia and New Guinea.

The groups of cerambycids detailed above show one genus in common between Australia and New Caledonia, and none between New Guinea and New Caledonia. However, in the Tmesisternini complex (Fig. 5), a closely knit group of several tribes of the cerambycid subfamily Lamiinae, relationships between New Guinea and New Caledonia, and (again) between New Caledonia and New Zealand, are clearly shown. Karny also noted that his groups of gryllacridids showed New Caledonia to be more closely related to New Guinea than to Australia. The tribes of cerambycids shown in Figure 5 include a total of a few hundred species and are comprised of peculiar, conspicuous beetles of medium to large size. Furthermore, the very small number of species of Homonoeini known from the Malayan Subregion (and one in Ceylon), and the two or three species of Bumetopiini known from north of the Philippine Subregion, are not likely to be greatly increased by further collecting, whereas more are continually being found in New Guinea. Therefore, statistically these groups may bear even more weight when our faunal knowledge is improved. It is possible that this complex is very old, though most workers have considered it specialized. Its absence on continental Asia suggests, again, that it might be a primitive group now extinct there, although if the age of part of New Guinea suggested by Cheesman (1951) is correct, the group might have evolved locally.

The generic ranges in the leaf beetle subfamily Cryptocephalinae (Fig. 6) also appear to emphasize the boundary north of Australia (excepting Cape York Peninsula) and the modified Wallace's Line. However, New Caledonia appears to be more closely related with New Zealand. The genus common to Australia and mainland Asia (*Cryptocephalus*) is practically cosmopolitan, although absent in New Zealand and Polynesia. The genus common to Fiji and mainland Asia (*Coenobius*) is widely distributed in the Old World but is absent from the Australian Region. Another genus, recorded from Australia and Fiji, is not shown and requires further study. Australia possesses nearly one-half of the world genera in this subfamily.

In the leaf beetle subfamily Hispinae (Figs. 7 and 8) the contrasts are somewhat similar, except that the Philippines appear to have four genera in common with Borneo which are not found in Celebes or New Guinea, and only two found in the Philippines and New Guinea which are not in Borneo. Nine genera occurring in Borneo are absent in the Philippines, but one of these also occurs in Celebes. Eight genera of this specialized subfamily are found in Celebes, nearly three times as many as occur in the Australian Region. The subfamily is absent from New Zealand, and only four genera extend into Polynesia. Two genera found east of the modified Wallace's Line occur also in the Mascarenes or Madagascar. The New Caledonian and Samoan genera are relatives of the one extending to the Mascarenes (*Brontispa*).

The chrysomelid subfamily Cassidinae similarly is absent in New Zealand, is poorly represented in Australia exclusive of Cape York Peninsula, and has most of its Philippine genera common to the Greater Sunda Islands (Gressitt, 1952). The subfamily is also absent in Tasmania and in Polynesia except for New Caledonia, if one excludes a species (living on the sweet-potato) that has been introduced into Samoa and two others introduced into western Micronesia (Gressitt, 1955). Among other subfamilies of Chrysomelidae, Australia possesses a considerable proportion of the genera of Sagrinae,

but a rather small proportion, or none, of most of the remainder.

The broad-nosed weevil tribe Pachyrrhynchini presents some interesting evidence in regard to the relationships of the Philippine fauna with that of the Greater Sunda Islands and New Guinea. This conspicuous group of weevils is centered in the Philippines (Fig. 9), with 160 species on Luzon, 110 in the central Philippines, and 41 on Mindanao. There are practically no species west of the Philippines proper, but a moderate number in the Papuan Subregion, and interestingly, only one known from Celebes. This again suggests Philippine-Papuan relationships, or at least some exchange. The evidence in this group, among other animals, together with botanical evidence, was used by Dickerson, Merrill, and others (1928) in following Huxley (1868) in modifying Wallace's Line to go west of the Philippines, between the Sulu Islands and Borneo, and between Mindoro on the east and the Calamian Islands (Busuanga) and Palawan on the west, and then between Luzon and Taiwan. Possibly in the long run the biota of the Philippines will prove

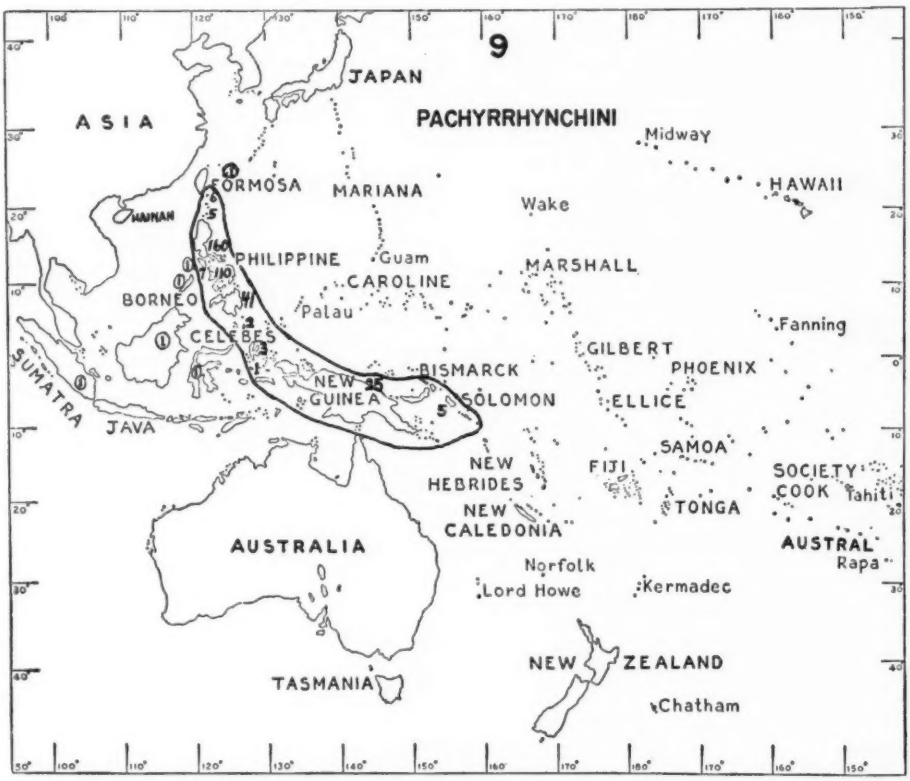

FIG. 9. Distribution of the weevil tribe Pachyrrhynchini. This conspicuous group has one species in the southern Ryukyu Islands, two on Samasana, six on Botel-Tobago, five in the Batanes, 160 on Luzon, seven on Mindoro, and only one each on Busuanga, Palawan, Borneo, Sumatra, and Celebes. Southward from Luzon there are several each on the islands of the central Philippines, 41 on Mindanao, one or two each in Talaud and Sanghir, three in the Moluccas, about 25 in New Guinea, and five in the Solomons.

to be more closely related to that of Borneo than to that of the Papuan Subregion, and Wallace's Line maintained between Celebes and the Philippines, as indicated for many groups. However, many of the groups I have studied lend weight to the above modification. Possibly a forking of Wallace's Line to branch both south and west of the Philippines proper, as shown in the subregion boundaries (Fig. 1), may be the solution. The Pachyrrhynchini extend northward, with five species in the Batanes, six on Botel-Tobago (Kotosho, Lan-yu) just east of the southern tip of Taiwan, two on Samasana Island (Kashoto, Lu-tao) just to the north of Botel-Tobago, and one in the southern Ryukyu Islands. Kano (1931*b*, 1935*b*) further modified Wallace's Line to go northward between Botel-Tobago and Samasana on the east, and Taiwan on the west, thus putting these two islands in the Philippine Subregion, and separating them from Taiwan and the Ryukyu Islands. I concur with this move, at least in the matter of putting these islands in the Philippine Subregion. Of 100 species of beetles on Botel-Tobago, only 11 occur also in Taiwan and seven in the Ryukyus, whereas 46 also occur in the Philippines (Kano, 1931*a*, 1935*b*; Gressitt, 1951*b*).

Taiwan has a fauna differing greatly from that of the Philippines. Of 465 species of cerambycids on Taiwan, only 2 percent are also found in the Philippines, and most of these may be traced through the Indo-Chinese and Malayan subregions, whereas 25 percent of the total are common to Taiwan and the mainland of Asia (Gressitt, 1951*b*). Hardly any genera are restricted to Taiwan and the Philippines together, most of their common genera being of widespread Oriental distribution.

The Ryukyu Islands also belong to the Indo-Chinese Subregion, and the chain formed a peninsula from South China, through Taiwan, during the Oligocene, late Pliocene, and early Pleistocene. At an earlier time, the chain had been connected with Japan, and there is a strong Palearctic element which the ancient mountain range transmitted to the mountains of Taiwan, where it is more extensively preserved. The Ryukyus have been more deeply submerged than at present, and there has been considerable depauperization of the fauna (Inger, 1947; Gressitt, 1951*a*, and in press).

Hainan Island is likewise part of the Indo-Chinese Subregion. It has a higher percentage of species in common with the mainland than does Taiwan and lacks the Palearctic elements found in the higher and more northern mountains of Taiwan. Less than 2 percent of the Hainan cerambycids occur also in the Philippines, and again these can be traced through the peninsula of Southeast Asia and the Sunda Islands (Gressitt, 1940). The southern border of the Indo-Chinese Subregion is a somewhat arbitrary boundary marking the gradual change to the almost uniformly tropical humid climate of the Malay Peninsula and the Greater Sunda Islands, i.e., the Malayan Subregion.

The insects of the Pacific require much more collecting and further taxonomic investigations and evolutionary studies. Only then will the insects provide an adequate basis for far-reaching conclusions about the zoogeography of these island chains, and particularly of New Guinea and the neighboring islands. Distribution patterns in different groups of animals often appear to be widely dissimilar because the dispersal, survival, and evolution of each is affected by different factors. Thus, final conclusions cannot be drawn on the basis of some limited, closely related groups as has been done in this paper. Particularly among insects, there is a need for further insight into their phylogeny, in terms of the historical geology, geography, ecology, and climatic history of the region.

Summary

1. Oceanic Pacific islands belong to the Oriental Region and, although assigned to a Polynesian Subregion, actually have a composite fauna which represents a grad-

ual attenuation of the fauna of the Papuan Subregion, and to a lesser extent of those of the Philippine Subregion, "Wallacea," and the Malayan and other subregions. Australian, American, and Holarctic influences are each relatively minor.

2. Faunal representation on Pacific islands demonstrates an attenuation, qualitatively and quantitatively, the more isolated islands having less harmonic faunae. Some groups of animals are more successful than others in colonizing islands distant from continents and continental islands.

3. Most insects on isolated oceanic islands are small and sedentary, often living in somewhat protected environments. The ancestors of most of them could plausibly have been carried to the islands by natural over-sea dispersal—by winds or floating trees, or by birds.

4. Among the groups widely represented on these oceanic islands are weevils, other small beetles living in dead plant materials, other small insects, and certain groups of land snails. Animals generally absent on islands distant from continents are mammals, land snakes, amphibians, water insects, fragile-winged insects, and most types of large insects, most butterflies, and many soil insects.

5. Studies to date in two of the principal families of phytophagous beetles indicate that those forms (mostly nocturnal as adults), living in dead twigs, dead logs, and seeds, and those mining in leaves, are more widely distributed than those boring in living plants, those feeding on roots in the larval stage, and those with unprotected exposed larvae on leaves or in soil.

6. These studies also suggest, as indicated by Mayr for birds, that Fiji, New Hebrides, and New Caledonia are oceanic islands, as they lack so many higher categories represented in the Solomon Islands and New Guinea; and also that there have been no very large bodies of land in the central Pacific. The present fauna of these oceanic islands does not require land-bridges or former continents to explain its origin.

7. Land snails on oceanic Pacific islands appear to include at least three endemic families, contrary to the situation in other land animals. Some of the relationships appear to be Indo-Malayan, some perhaps Neotropical, and some Holarctic. Their ancestors were probably introduced by birds or by wind-blown or floating debris.

8. In several groups of beetles, and in some snails, there are distinct relationships between the Micro-Polynesian fauna and that of islands in the western Indian Ocean, such as the Mascarenes and Seychelles, or even Madagascar. In most of these the groups concerned are absent from continental Asia and even from the Malayan Subregion, although some do occur in New Guinea. This suggests a survival of primitive forms which have become extinct in continental areas where more advanced forms exist.

9. The beetles studied suggest that the New Guinea fauna is more closely related to that of the Philippines than to that of the Sunda Islands, and that the differences between the faunae justify the modifying (or bifurcation) of Wallace's Line to go northward between the main Philippines on the east and Palawan and Borneo on the west, and further between Botel-Tobago and Samasana on the east and Taiwan on the west.

10. Further studies on insects, particularly of the New Guinea area, are needed fully to clarify faunal relationships in this region, because the Asiatic connections of New Guinea are so ancient as to antedate the evolution of most higher mammals and some birds. The influence of later connection with Australia is thus more strongly emphasized in higher vertebrates than in most insects.

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(Concluded on p. 47)

Modifications of the International Rules of Zoological Nomenclature Proposed since the 1953 Copenhagen Congress

W. I. FOLLETT

AT THE XIV International Congress of Zoology, held at Copenhagen during 1953, Professor J. Chester Bradley, President of the International Commission on Zoological Nomenclature, was delegated the task of drafting a revised set of nomenclatural rules, which would embrace the decisions reached at Copenhagen, the provisions enacted by the 1948 Paris Congress, and the International Rules theretofore in effect (Hemming, 1953, pp. 96–97). Presumably, Professor Bradley's draft is now in press. Meanwhile, a number of modifications of the existing rules have been proposed.

Retroactivity of a New Rule

It has been proposed that no new rule shall retroact in such manner as to overturn the well-established usage of any name.

There are certain rules with which this provision would conflict, such as the following:

1. An emendation, although in general use, if not approved in an Opinion and not qualified as a Valid Emendation, is to be rejected unless an author resorts to the protest procedure (Hemming, 1953, pp. 45–46).

2. A name bearing a diacritic mark is to be rewritten in accordance with a schedule of equivalent letters, to be annexed to the rules (Hemming, 1953, pp. 57–58).

3. A specific name originally published as a hyphenated word is to be rewritten as a single unhyphenated word (Hemming, 1950, p. 198).

4. A specific name consisting solely of a man's unchanged surname (e.g., *cerisy*) is to be corrected by adding the appropriate genitive suffix (Hemming, 1950, pp. 251–252; 1953, p. 52).

5. A generic name formed in violation of any mandatory provision of Article 8, or a specific name formed in violation of any mandatory provision of Article 14, is to be corrected by subsequent authors (Hemming, 1953, pp. 47–48, 53).

It may be noted further that the provision, as proposed, would necessarily involve subjective interpretation of the expressions "new rule" and "well-established usage." For example, those zoologists who refused to follow the rule of the first reviser, even before it was abrogated in 1948 (Follett, 1953*a*, p. 389), might contend that upon its reenactment with certain modifications in 1953 (Hemming, 1953, pp. 66–67), it became a "new rule," which they were required to disregard in favor of their "well-established usage" based on position precedence.

The phraseology of the proposed provision should therefore be reconsidered.

Type Genera in Synonymy

The provision enacted at Copenhagen that where the name of the type genus of a Family Group taxon must be changed because it is a junior synonym, objective or subjective, the name of the Family Group taxon based on the name of that type genus is not to be changed (Hemming, 1953, p. 36) has been criticized by Arkell (1954, 1955) but defended by Sabrosky (1954).

If this provision were retroactive, the objection would appear well founded. However, the proposed restriction on retroactivity, mentioned above, would seem to eliminate such objection. Furthermore, it is provided that "The naming of units belonging to the Family-Group of categories shall be governed by priority, except that, in cases where priority is in conflict with current usage, current usage is to be maintained, wherever, in the opinion of the individual taxonomist, this would lead to greater stability and universality of nomenclature than would the strict application of priority" (Hemming, 1953, p. 33).

If the provision for retention of the Family Group name should be revoked, the door would be opened to a flood of family-name changes in the future, based upon the subjective reevaluation of generic limits.

Gender of Generic Names, in Different Fields of Zoology

It has been proposed that the International Commission be granted power to prescribe, in disregard of grammatical requirements, that a certain generic name or nominative suffix be arbitrarily deemed, in one or more fields of zoology, to have a gender different from that prescribed for it in other fields (Hemming, 1955, pp. 256–259).

Opposed to this proposal are the following considerations:

1. Two hundred eighty members of the Society of Systematic Zoology, comprising 90% of the 312 who replied to a questionnaire distributed to the entire membership during 1952, voted in favor of uniform rules of nomenclature for the whole of zoology (Follett, 1953*b*, p. 456).

2. As a result of the deliberations of the Colloquium on Zoological Nomenclature, which preceded the XIV International Congress of Zoology at Copenhagen in 1953, the following statement was published: "The Colloquium has taken favourable note of a document submitted to the International Commission urging the importance of maintaining uniform Rules of Nomenclature for the whole Animal Kingdom, and it takes this opportunity to draw attention to the fact that many of its recommendations have been inspired by this principle" (Hemming, 1953, p. 85).

Gender of Generic Names Comprising Compounds Based on Classical Greek Words

The present rules for determination of the gender of generic names based on classical Greek words provide in effect as follows (Hemming, 1953, p. 50):

1. Where one of the comprised words is an adjective and the other a noun, the name takes the gender of the noun.

2. Where both comprised words are nouns, one of which is a noun with verbal force, the name takes the gender of the noun having verbal force.

3. Where both comprised words are nouns and neither has verbal force, the name takes the gender of the second noun, save exceptionally where (as in *Hippopotamus*) it is evident that the first noun is primary and the second strictly adjectival.

It has been protested that these provisions are complex and difficult to understand, and that since the gender of a compound word is almost invariably that of its final term, a more objective rule would result from basing the gender invariably upon the final term, for zoological purposes.

Compound Nouns Used as Specific Names

Complaint has been made that much uncertainty exists by reason of the failure of the rules to specify whether a Greek compound noun (e.g., *xanthostigma*) or a Latin compound noun (e.g., *atricauda*), when used as a specific or subspecific name, is to be treated as a noun or as an adjective. It has been indicated that many such compounds may properly be treated as adjectives (Miller, 1897). On the other hand, such compounds have elsewhere been referred to as nouns in apposition with the generic name (Hemming, 1950,

pp. 240–242, 296). The rules should clearly provide either (1) that such a compound is to be treated invariably as a noun in apposition with the generic name, or (2) that it is to be treated invariably as an adjective, or (3) that where the usage of the original author indicates that he regarded the compound as a noun or as an adjective, the name is to retain the character so indicated, and that where the usage of the original author is not conclusive, a subsequent author, as first reviser, may permanently establish the name as a noun or as an adjective.

Perhaps the simplest solution would be to provide that such a compound is to be treated invariably as a noun in apposition with the generic name. This would enable all subsequent authors to retain the original orthography, and would eliminate the necessity of a change in termination when such a specific name is combined with a generic name of a gender different from that involved in the original binomen.

Prénoms

Provisions for the formation of a specific name based on the prénom (Christian name, or given name), of a modern person, as contrasted with the surname, were enacted by the 1948 Paris Congress (Hemming, 1950, pp. 200, 203, 205). These provisions appear to have been overlooked by the 1953 Copenhagen Congress, or to have been reduced to the status of a recommendation (Hemming, 1953, pp. 52–53). In either event, the proper treatment of a specific name based on a prénom, heretofore published, is not now covered by any rule. This situation should be clarified, preferably by a distinct statement that the rule involving surnames applies as well to prénoms.

Notation of Hybrids

The rules provide that the notation of a hybrid may be given in several ways; in all cases the name of the male parent precedes that of the female parent, with or without sexual signs (Article 18; Hemming, 1950, pp. 212–213):

1. The names of the two parents are united by the multiplication sign (×). Example: *Capra hircus* ♂ × *Ovis aries* ♀ and *Capra hircus* × *Ovis aries* are equally good formulae. A hybrid between two species of the same genus may be indicated by placing in parentheses, after the generic name, the specific names of the two parents, united by the multiplication sign. Example: *Tetrao* (*tetrix* × *urogallus*).

2. Hybrids may also be cited in the form of a fraction, the male parent forming the numerator and the female parent the denominator. Example:

$$\frac{\textit{Capra hircus}}{\textit{Ovis aries}}$$

This second method is preferable in that it permits the citation of the person who first published a description of the hybrid as such. Example:

$$\frac{\textit{Bernicla canadensis}}{\textit{Anser cygnoides}}\ \text{Rabé}$$

3. The fractional form is also preferable in case one of the parents is itself a hybrid. Example:

$$\frac{\textit{Tetrao tetrix} \times \textit{Tetrao urogallus}}{\textit{Gallus gallus}}$$

or

$$\frac{\textit{Tetrao tetrix}}{\textit{Tetrao urogallus}} \times \textit{Gallus gallus}$$

4. Where the identity of either parent of a hybrid is uncertain as to species or sex, the hybrid takes provisionally a specific name, subject to all provisions regarding specific names, as if it were a true species rather than a hybrid, but the multiplication sign must precede the generic name (e.g., × *Coregonus dolosus* Fatio).

These provisions seem complicated, obsolete, and in need of a thorough revision. The recommendation that the name of the male parent precede that of the female violates the practice of most geneticists and overlooks the fact that ordinarily the sex of a parent of a natural hybrid is unknown. For natural hybrids, an alphabetical sequence is more advantageous.

The requirement that a quasi-specific name be applied to any hybrid of which either parent is unidentified as to species or sex is contrary to good practice.

It has accordingly been proposed that this section of the rules be replaced by a provision to the effect that a name applied to a hybrid as such shall not be available for either of the parental species, and shall have no status in nomenclature.

Type-Locality Restriction

It is now provided that where a type locality is considered insufficiently precise and there are inadequate data on the label of the type, the type locality may be restricted by a first reviser, and may be further restricted by a subsequent reviser. As between two or more restrictions, priority is to apply, except where the later author further restricts the locality specified by the earlier (Hemming, 1953, pp. 26–27).

It would appear proper to add a provision similar to that contained in the rules regarding neotypes (Hemming, 1953, p. 29), to the effect that the restricted or designated type locality must be consistent with all available information on the species, and that a restriction or designation that is not consistent with such information is not to be binding upon subsequent authors.

Undetected Homonymy

The 1948 Paris Congress enacted a rule (Hemming, 1950, p. 345) to the effect that where two taxa bearing identical specific or subspecific names were originally described in, or later referred to, different genera bearing identical generic names but the fact that those generic names were homonyms of each other had not then been detected, the later-published specific or subspecific name is not to be rejected as a homonym of the earlier-published name.

This provision does not take into account the possibility that the homonymy, though detected, may have been disregarded. Furthermore, it is not clear whether the homonymy must have been undetected by authors in general or merely by the author of the junior homonym. Determination of whether any author had ever detected the homonymy might involve much loss of time and might be largely subjective. A simpler and thoroughly objective procedure would remain if this exception to the rules of homonymy were deleted. The situation contemplated by this exception could best be rectified under the Commission's Plenary Powers.

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Points of View

A Note on the Systematic Position of the Mesozoa

The Mesozoa are a small group of planuloid worms that are parasitic within various invertebrates. Structurally, they are the simplest of Metazoa, consisting of a solid core composed wholly or in part of reproductive cells, encased in a surface layer of ciliated cells. They are thus structurally of the grade of a planula larva. The group was named in 1876 by Van Beneden with the intention of indicating his belief that their grade of structure is intermediate between that of Protozoa and typical Metazoa. This viewpoint was adopted by Hartmann (1925) and, very tentatively, by Hyman (1940). On the other hand such investigators as Whitman (1883), Stunkard (1937), and McConnaughey (1949, 1953) regard the simplicity of the Mesozoa as not at all primitive but the result of extreme parasitic degeneration. This viewpoint has been strongly urged by Stunkard (1954) but he failed to answer any of the arguments of Hyman (1940) against it. McConnaughey and McConnaughey in a later paper (1954) seem to lean a little closer to the viewpoint of Hyman. Considerable importance attaches to this difference of viewpoint. If Stunkard is right, then the Mesozoa are simply a group of degenerate flatworms of no theoretical importance. If the view that the Mesozoa are extraordinarily primitive Metazoa is right, then as Hyman (1940) has said "the group would be of the utmost phylogenetic significance, as a stage between Protozoa and Metazoa. They would furnish proof that the first step in metazoan organization is the relegation of reproductive cells to the interior, that the original metazoan had a solid, not a hollow construction, and that the Gastraea theory of Haeckel is definitely erroneous . . . the author believes that their characters are in the main primitive and not the result of parasitic degeneration."

Mesozoan Life Cycles

The Mesozoa comprise two groups, the Orthonectida and the Dicyemida. The salient features of their life cycles have been recently presented by Stunkard (1954) and McConnaughey and McConnaughey (1954), the latter with illustrations, but a brief summary is in order here. Orthonectids exist in various marine invertebrates as parasitic plasmodia that give rise to the adult males and females. These escape into the sea as minute ciliated organisms composed of an outer ciliated epithelial layer of a definite number of cells, enclosing an inner cell mass made up entirely of sex cells. Following insemination the fertilized eggs develop inside the females into ciliated embryos that escape as larvae composed of a few germinal cells encased in ciliated cells. These invade the host invertebrate where they disintegrate, releasing the germinal cells, and these develop into plasmodia.

The life cycle of the dicyemids is more complex and not yet fully elucidated. The known stages parasitize the kidneys of cephalopods, which become infected shortly after hatching. Here they occur as vermiform organisms (nematogens) consisting of a single large axial cell, enclosed in a covering of ciliated cells, definite in number and arrangement. The axial cell contains reproductive cells of the nature of agametes (axoblasts) that develop into a new generation of nematogens, and this process is repeated for a number of generations. As the host cephalopod matures sexually, the parasites undergo a change of phase, becoming or producing what are termed rhombogens.

These differ from nematogens only in their products which are known as infusorigens, and which are simply groups of cells inside the rhombogen. The researches of McConnaughey (1951) support an earlier view that these infusorigens are hermaphroditic individuals but it is at least possible that the rhombogens are the sexual individuals of the dicyemids and that the infusorigens are their hermaphroditic gonads. At any rate the infusorigen consists of a central cell in which sperm develop and peripheral cells that become eggs. The fertilized eggs develop in situ into ciliated larvae known as infusoriform larvae that escape into the sea by way of the host urine. The infusoriform larva is of complicated construction, consisting of a definite number of cells, some ciliated, some with inclusions; an interior cavity, the urn, contains a group of four cells which are of reproductive nature, each containing two nuclei and a germinative cell. The infusoriform larvae swim about actively, although they do not feed, and may live for three days to a week in the laboratory. Their fate is unknown and constitutes the unelucidated part of the dicyemid life cycle. Presumably they enter an intermediate host in which some sort of development occurs for the earliest stage yet found in the young cephalopod is a nematogen, differing from ordinary nematogens mainly in having two or three axial cells.

Comparison of Dicyemids and Platyhelminths

Stunkard (1954) insists strongly that the Mesozoa are degenerate flatworms but gives for the most part only generalities as reasons. As specific evidence he gave mainly a comparison between the miracidium and the infusoriform larva. This comparison is enhanced by the finding that the latter also comes from a fertilized egg, something that had not been established at the time of Hyman's 1940 account. It is also true that both types of larvae have a constant and definite number of surface cells, and that they both contain germinative cells, but otherwise the comparison is not very convincing. The two types of larvae certainly differ markedly in structural details. As regards other correspondence between mesozoans and digenetic trematodes, Stunkard refers to the asexual multiplication in both groups and to the similarities of cleavage pattern. He remarks that in both orthonectids and digenetic trematodes the number of progeny is increased by polyembryony, but polyembryony occurs in so many different types of animals that it can hardly serve as an argument for relationship. Since the infusorigen produces the infusoriform larva by a sexual process it would have to correspond to the sexually mature trematode with which it has no resemblance of any kind. Even if, as suggested above, the rhombogen is actually the sexually mature dicyemid, it also does not resemble a mature trematode. But some resemblance can be found between the adult orthonectids and the most primitive free-living flatworms, namely the Acoela, and this supports the concept of the planuloid nature of the Mesozoa.

Parasitism and Degeneration

Stunkard's major argument is that parasitism leads to degeneration. Seemingly this somehow proves to his mind that the Mesozoa are degenerate flatworms. He quotes Whitman (1883) as follows:

> . . . when we find an animal in the form of a simple sac, filled with reproductive elements, secured by position against enemies, supplied with food in abundance, and combining parasitism with immobility, we have strong reasons for believing that the simplicity of its structure is more or less the result of the luxurious conditions of life which it enjoys, even if its development furnishes no positive evidence of degeneration.

At the outset, it may be said that such a declaration has little forensic value in the present instance because it assumes the very point that is under debate. Further the dicyemids can hardly be de-

scribed as simple sacs, in view of the differentiation of their surface cells, and they are not immobile. Stunkard's further statement that holozoic nutrition has been supplanted by parasitism appears not entirely correct for the surface cells of the dicyemids phagocytize and digest nutritive particles. Many examples can be cited in which parasitism has not entailed notable simplification of structure. There are, for instance, the mastigote flagellates that inhabit the digestive tract of termites and cockroaches, and the ophryoscolecid and cycloposthiid ciliates in the digestive tract of mammals, all of which are among the most highly organized and complex of all Protozoa. The umagillid rhabdocoels that inhabit the digestive tract of echinoderms have undergone little change from their free-living relatives. Parasitic nematodes are not strikingly different from free-living ones.

Simplification of parasites results because the parasite uses the organ systems of the host and hence continued integrity of its own organ systems is not favored by selection pressure. In organisms that have not yet reached the organ grade of construction as the Protozoa (and possibly the Mesozoa) this factor could not be operative, hence complex ancestral stages need not be assumed for parasites now at the tissue level of construction or lower, unless other evidence requires it. The rhizocephalan barnacles and enteroxenid snails are certainly striking examples of extreme parasitic degeneration but these are highly organized animals that have become internal parasites, hence cannot use most of their structural features. They indicate their systematic status by producing typical young but it cannot be said of Mesozoa that they indicate a descent from flatworms by producing typical flatworm stages. If a planuloid animal should adopt a parasitic mode of life, it would seem that it could be simplified further only by reverting to a protozoan status. It is difficult to imagine what sort of selective factor could favor this.

Mesozoa as Primitive Metazoa

The positive arguments brought forward by Hyman for the primitive status of the Mesozoa are ignored by Stunkard in his review. At the outset it may be mentioned that the Mesozoa, as endoparasites, occupy a habitat quite comparable to that of many trematodes. Yet the latter have not even approached the degree of degeneration postulated by Stunkard for the Mesozoa and it is difficult to conceive of a selective factor that could act so much more effectively upon one group than upon the other. Stunkard states that the Mesozoa are undoubtedly a very ancient group in which there has been time for the extreme of parasitic degeneration to occur; but if they are descended from parasitic flatworms they cannot be any more ancient than the latter, in fact, must be less ancient.

Hyman emphasized the retention of cilia as a primitive character of Mesozoa. Mesozoa share this character with the *larvae* of parasitic flatworms but these quickly lose their cilia. Why this primitive character should be retained in the adult form by what are alleged to be the most degenerate of all parasitic flatworms is difficult to understand.

Another point made by Hyman is that the adult orthonectids are well known and have no characteristics in common with adult parasitic flatworms, although as already suggested they are not wholly unlike the free-living acoel flatworms. The latter also have no definite entoderm and no digestive system. Stunkard notes that adult orthonectids do not feed, but this is not uncommon in the adults of animals that have parasitic young; note, for example the mermithid nematodes and the gordiacean worms. One may also recall that mayflies which do not feed as adults do not have parasitic young. Stunkard's statement that the adult orthonectids are highly modified appears to be reasoning in a circle as it assumes that which is under dispute.

Stunkard cites cell constancy as a sim-

ilarity between Mesozoa and parasitic flatworms. Cell constancy applies to the nematogen and rhombogen stages of dicyemids (which seem to be the adults), to the infusoriform larvae, and to adult orthonectids as well, whereas among flatworms it is characteristic only of the trematode miracidium. This is not a very convincing comparison. It should be mentioned, too, that Van Cleave (1932) in his general review of the phenomenon of cell constancy found it to be scattered throughout the animal kingdom in such a haphazard manner that no phylogenetic conclusions could be justified.

Conclusion

It is not the intention of this paper to claim that the Mesozoa actually are primitively simple rather than extremely degenerate flatworms but rather to point out that Stunkard's argument (1954) in favor of the latter view is far from convincing and fails to answer data that favor the former view. Stunkard's statement that the "simplicity of structure in mesozoans is clearly secondary and the result of parasitism" is simply an assumption that cannot be proved in the present state of knowledge. In support of his view Stunkard for the most part adduced generalities about parasites and cited very little in the way of specific comparisons between mesozoans and parasitic flatworms. Stunkard believes that "from a hypothetical, generalized planuloid progenitor it is possible to derive each of the existing groups of the phylum Platyhelminthes. Accordingly it appears that the Turbellaria, Mesozoa, Cestoda, and Digenea have descended concomitantly from a common ancestral group of planula-like progenitors." But does not this reverse the previous conclusion that the Mesozoa are degenerate flatworms? Does not this statement lead to the concept that the Mesozoa have remained close to the "generalized, planuloid progenitor?"

The most logical taxonomic treatments for the Mesozoa in the present state of knowledge are to place them in *sedis incertae;* or to accept their morphology at face value and give them phylum status without further theoretical implications as did Hyman (1940). By definition a phylum is an assemblage of animals sharing a basic structural plan that is dissimilar to the plan of all other assemblages and that is difficult to derive from any other. The Mesozoa meet the criteria of this definition and hence their status as an independent phylum is defensible until new and more conclusive evidence is brought forward in support of their inclusion in the Platyhelminthes as demanded by Stunkard.

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On the Discovery of a Second Member of the Crustacean Subclass Cephalocarida

In September, 1953, in the course of a benthic sampling program carried out in northern San Francisco Bay, we collected a small crustacean which we could not identify. In searching for information to help us identify the animal we learned that Dr. Howard L. Sanders had collected a similar animal from the muddy bottom of Long Island Sound. Sanders (1955) later described his find as a new genus and species, *Hutchinsoniella macracantha,* and erected for it the new subclass Cephalocarida. To date we have collected but three specimens of our cephalocarid, while Sanders based his description on eight specimens, and we are informed by him that he now has collected more than 50 specimens and has extended the range to Buzzards Bay, Massachusetts. It is interesting to note that our first collection of a cephalocarid followed Sanders' original collection by only one month.

The San Francisco Bay specimens resemble *Hutchinsoniella,* but with differences which suggest that we are dealing with a different species or even a higher taxon. The most obvious difference between the east and west coast forms lies in the number of body segments; *H. macracantha* possessing 19 and ours 20, excluding the telson. The structure and ornamentation of the telson also provide major points of difference. A study of our specimens has led us to the conclusion that our animals are immature. To support this conclusion we cite the fact that, although each specimen has the same number of body segments, one has six postcephalic appendages and a rudimentary seventh, the second has four and a rudimentary fifth, and the third specimen has eight, plus a rudimentary appendage on the tenth segment (we are at a loss to explain the absence of appendages on the ninth segment). In comparison, *Hutchinsoniella* has 10 postcephalic appendages, the ninth reduced and the tenth rudimentary. In crustaceans the body segments generally develop before their appendages appear and this fact, coupled with the larger number of appendages in *Hutchinsoniella,* clearly suggests that at least two of our specimens are not fully developed.

Our first problem is that presented by the nature of our specimens. We believe they are immature and we have but three individuals. We would like to describe this animal to add to the meager knowledge of this newly described group, but we feel our material is insufficient to describe the animal adequately. We have decided, therefore, that rather than present our animal as new and describe it incompletely, we must wait for further specimens to be collected.

The second problem and one with somewhat wider implications is that the Cephalocarida as a new subclass has none of the usual subdivisions in its makeup, and, therefore, we have no established characters to use as comparative data in evaluating the taxon of the specimens now in hand. The student of most groups has little problem when faced with a new taxon. He has available to him, as yardsticks, all of the differences recognized in the various orders, families, genera, etc., within his group. In the cephalocarids we find we skip from subclass to family to genus to species, and all are monotypic. We can look to the definitions within other groups of Crustacea or even to other groups of arthropods for help, but there is little satisfaction in discovering that in a group as large and varied as the Copepoda (perhaps not too distantly related to the Cephalocarida), when the segmentation is complete, there are always 16 somites present. In the Copepoda, however, there is often a difference of one segment between males and females of a species, the males having one more segment than the female. Among the copepods reduction in number of body somites, other than the just-mentioned sexual difference, seems to

be closely associated with sessile or parasitic habits, and variations in number of somites characterize such groups as orders.

The cephalocaridan from San Francisco Bay seems to be a free-living member of the benthos as does *Hutchinsoniella*, so that our information from the Copepoda suggests that we may be dealing either with a higher taxon or with a sexual difference. At the time Sanders described *Hutchinsoniella* he commented (p. 64) that, "It is not improbable that all the specimens are females," and in response to our request for further information regarding possible sexual differences we were informed by Dr. Sanders that of more than 50 specimens which he has now observed, all seem to be females. We therefore do not know whether or not to expect the sexes of the cephalocarids to be characterized by different numbers of somites. The sex(es) of our three specimens is unknown.

The cephalocarids from San Francisco Bay seem clearly to be specifically distinct from Sanders' species, unless (improbably) we have the males and he the females of a single species. However, the nature of the differences which we have discovered suggests to us that we are dealing with a difference, perhaps generic, familial, or even, possibly, ordinal. That we cannot readily determine the systematic level of the differences we have observed, brings home the (at times) arbitrary nature of such categories as genera and families, and until numerous species of this group have been described, decisions as to what constitutes a genus, for example, will be no more than careful guesses. With time, and the description of more species, genera of cephalocarids may emerge as definable and useful categories, and the same, we presume, would be true for taxa above the genus. However, if no more species of this group are ever discovered, generic concepts would then, we presume, never be developed beyond our own decision that our form is generically distinct from *Hutchinsoniella*.

From this situation there emerges a premise which is borne out in the larger groups such as Protozoa, Mollusca and Arthropoda where it is seen that, in general, the number of supraspecific taxa bears a direct relationship to the number of species known for the group. There are, however, exceptions as in the class Polychaeta of the Annelida where, in spite of morphological diversity and a profusion of species, orders are difficult to recognize. In the opposite direction we might note the apparent exception of the rather small class Scyphozoa of the Coelenterata, where with only about 200 valid species, five orders are recognized.

To conclude, we believe that we must be cautious, because of our scant and immature material, in presenting our cephalocarid as a new systematic entity, and that, in a group without established categories to provide useful yardsticks, any decision regarding the systematic value of observed differences between known forms can only be interpreted in an arbitrary fashion.

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A Suggestion for the Standardization of the Higher Systematic Categories

Several attempts at standardization of the higher taxa have been made in the past, e.g. Poche (1938), which have not been adopted. According to Simpson (1945, p. 25) the lack of general interest in Poche's effort was due, in large measure, to its impractical nature. It comprised over forty-two supraspecific cate-

gories and proposed endings for all of these major groups. Regardless of this it is herein suggested that the time has come for systematists to consider actively standardization of the systematic heirarchy. A system is herewith presented which can be used as the basis for such standardization.

The assumptions supporting this suggestion are: (1) A standardized system would be beneficial to systematics and zoology in general; (2) To be satisfactory a system must be simple, logical and consistent and yet natural enough to indicate as much phylogeny as possible.

Studies of various phases of systematics reveal that a need exists for standardization and stabilization of the systematic heirarchy. In the course of such study one is met by the usual phylum, class, order, family and genus (and their super- and subcategories), plus an array of others of less common usage, e.g. grade, cohort, phalanx, branch, division and tribe. Schenk and McMasters (1948) give a partial list of taxa, forty-eight items, which have been used at one time or other. These authors, also, stress the lack of standardization existing in the higher categories. The little-used taxa mentioned therein recur from time to time in taxonomic works and add to the burden and confusion with which the systematist must cope. To complicate the picture further, at least six of these categories have been employed at more than one level in the heirarchy, e.g. division, branch, tribe. A study of Pearse (1949) confirms this duplication.

Although the natural species groupings and their relationships are objective, the taxa as now known and used are, in some measure, subjective. The factors responsible for this subjectivity are several and have been adequately discussed by other authors (see Simpson, 1945; Mayr, Linsley and Usinger, 1953). It is because of this degree of subjectivity that standardization can be accomplished without affecting the naturalness of the system.

In accordance with the above considerations the following scheme of taxa is suggested for adoption as the standard:

Kingdom
Subkingdom
Superbranch
Branch
Subbranch
Superphylum
Phylum
Subphylum
Superclass
Class
Subclass
Superorder
Order
Suborder
Superfamily
Family
Subfamily
Supergenus [1]
Genus
Subgenus
Superspecies
Species
Subspecies

The obligatory taxa of this scheme are kingdom, branch, phylum, class, order, family, genus and species. The intermediate taxa are classed as optional by Simpson (1945) and are so considered here. If there proves to be need for additional intermediate categories to accommodate certain more evolutionarily diversified groups it is suggested that the group indicated by the prefix infra-, as proposed by Simpson (1945), Romer (1945) and others, be interposed between the sub-category preceding it and the super-category following it. Infra- can be used at any level of the scheme.

As can be seen this system, which is essentially a compilation and rearrangement, includes no unknown groups. Indeed, all of the groups, with the possible exception of supergenus, are in use to-

[1] The categories tribe (mentioned in Item 47, Part 2, Document 1 of the recent Copenhagen Decisions) and subtribe as employed by Simpson (1945) may be used to replace infrafamily and supergenus respectively, if desired.

day. Basically, it includes twenty-three systematic categories, twenty-one of which are supraspecific. If the infragroupings are used, a total of twenty-eight supraspecific taxa are available.

Discussion of the Individual Taxa

Kingdom and subkingdom are currently in wide use and appear to be acceptable to the majority of taxonomists.

Branch with its super- and sub-categories are also in use, though less widely accepted than the kingdom complex. This taxon is actually an alteration of the position of the same category as employed by Hyman (1940). Branch is placed in this position to fill the need for an obligate taxon between the levels of kingdom and phylum. Hyman's categories Grade and A., B. and C. have been left out of the present scheme.

Superphylum, with phylum and subphylum, is widely used in many well-conceived systems, and because it is useful and necessary will probably persist in spite of the minor objections raised against it. It is logical and necessary to the present scheme.

The categories between superphylum and supergenus are so generally utilized as to require no discussion or explanation.

The categories division, phalanx, cohort etc. are omitted from the present scheme for the sake of simplicity and other reasons put forth in the present paper.

Supergenus has neither been widely used nor cordially received when it has been presented. The main objection seems to be that the prefix super- placed with genus has undesirable implications, i.e. semantic connotations. (See Schenk and McMasters, 1948, p. 4, for their rejection of this category.) Bearing in mind that systematic categories should not be regarded as possessing semantic connotations but should be accepted or rejected objectively, there can be no sound objection to the use of supergenus as a taxon. It is merely a logical extension of most currently accepted systems. The supergenus should be based on a type genus and come under the jurisdiction of the International Commission on Zoological Nomenclature. This, of course, would apply also to infragenus and infrafamily if they are used.

Genus and subgenus are both in use today. The former is universal and the latter found in many groups, e.g. fishes. Although Mayr (1942) and Mayr, Linsley and Usinger (1953) object to subgenus on the grounds that it is merely a catch-all for genera that some authors are too timid to completely subdue, it is herein supported as natural, logical, necessary and useful as any other subcategory. Simpson (1945, p. 24) supports its use.

The taxon superspecies is employed at the present time by several authors in different groups (see Mayr, 1942) but it is not in general usage. However it is a logical grouping of similar species and should carry no untoward semantic meanings. The subgeneric and superspecific names should be placed in a linear arrangement as above. It is felt that the use of subgenus and superspecies in a standard system would restore the collective nature of the genus and still permit the presentation of phylogenetically significant groupings. This would perhaps minimize the possible detrimental effects of the activities of the "splitters," who have created many monotypic genera, in that adequate infra-generic taxa with which to indicate significant differences between species groups would be provided. Important relationships would still be maintained. The "lumpers" would be encouraged to realize that there are intermediate groupings of species which should be recognized in any natural system. These two categories would be of use chiefly in taxonomic papers or other detailed works and need not burden the general zoologist.

The intermediate categories infra- are employed by several authors working in the better known groups (Simpson, 1945—mammals; and Romer, 1945—vertebrates in general) and are useful. It is

probable that they will prove of future value in the systematics of presently little-known groups when they have developed more. Their use, in place of the invention of new taxa, insures that the basic obligate categories will remain the same and obviates the necessity for the creation of unique categories for different animal groups.

General Discussion

The scheme presented herewith for consideration by zoological systematists as a standard system of higher categories is a logical and natural expansion of the scheme which is at present widely used and is wholly in keeping with the currently held biological concept of a phylogenetically significant taxonomy.

The reasons why standardization would be beneficial are: (1) Standardization will eliminate the use of unfamiliar and ambiguous taxa. (2) It is presumed that the time has arrived when the schemes proposed and utilized by workers in the different animal groups be brought into alignment. It is the writer's opinion that the use of unusual or variable categories in various groups, e.g. division and tribe in the Crustacea, cohort, in the Mammalia, is unwarranted. These irregular or infrequently used taxa render phylogenetic comparison somewhat difficult. Apparently one of the assumptions on which the creation and use of such categories is based is that the higher categories have precisely the same objective level in all groups and that, therefore, the introduction of these taxa into the systematics of groups which have attained different evolutionary levels is necessary. Actually, while it would be excellent if they were, the higher categories are not precisely equal, i.e. on the same level, in all groups, and are somewhat subjective in nature. That such taxa are not equivalent in different groups becomes even more apparent when it is observed that all of the animal groups have not evolved at the same rates nor for the same lengths of time. If these observations are valid it is not necessary to create unique taxa for the systematics of different groups in an attempt to preserve the precise relative systematic level of the other categories in those groups. The taxa suggested herein can be used, and are sufficient, for any group, provided that the intergroup phylogenetic disparities are recognized. (3) The use of the same systematic category at more than one level in the phylogenetic schemes of different animal groups would be eliminated by the adoption of this or a similar system. Schenk and McMasters (1948, p. 4) show that such duplication actually exists and Pearse (1949, pp. 13 and 18) employs division below both infraclass and subphylum on the respective pages. (4) The adoption of an adequate, natural, standard system would tend to minimize difficulties springing from the actions of the "lumpers" and "splitters" of taxonomy. (5) It is logical to contend that the sooner systematists actively control this phase of a rapidly expanding systematics by adopting a sound standard of higher categories, the more effective and better organized the subscience of systematics will be.

It is probable that the scheme suggested here is sufficient to accommodate any of the known groups of animals and will serve to indicate phylogeny as well, and as practically, as possible. It is thought that the use of many more taxa than herein suggested will be a hinderance rather than a help. However, should the need be felt at some future date, additional taxa can be added. Should this exigency arise only those logical categories which would be acceptable to a majority of systematists should be considered

The following classifications have been examined and it appears probable that with minor replacements and adjustments their schemes can be fitted into the present system: Hyman (1940), Brown (1950), and others for the invertebrates; Romer (1945), Simpson (1945), American Ornithologists' Union (1931) and Berg (1947), for the chordates; and Pearse

(1949), for the entire animal kingdom.

The fact that the present scheme, particularly some of the optional intermediate groupings near the species level, will be of most use to the systematics of the well-known groups, is no reason why such a standardized system should not be attempted. It would offer well established and standardized taxa into which the systematics of lesser-known groups could grow and it would also obviate the possibility of the creation of additional and disconcerting special categories for these expanding groups.

The present author is well aware that a single worker cannot possibly be familiar with all of the intimate details of the myriad animal groups which have been, and are being, studied. Although logic and utility are paramount in treating such partially subjective entities as systematic taxa, it is possible that other valid reasons (perhaps practical ones) will require that some emendations be made in the suggested scheme before its adoption. Because the subject under discussion is so basically important, the present, and any other, suggestions for standardization of the heirarchy should be studied thoroughly and critically before definite action is taken. It is probable that the criticisms and suggestions of many will be required before a satisfactory standard scheme can be established.

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Jordan on Rafinesque

The early French-American naturalist, Constantine Samuel Rafinesque (1783–1840), has earned a reputation among later taxonomic workers for describing species insufficiently in detail for positive recognition by others. This has led to much confusion and uncertainty in the taxonomic literature. Because of his erratic practices many have overlooked some of his works, including some valid contributions.

This past summer, while working through the papers of Frederic W. Putnam, who was an Assistant in Ichthyology at the Museum of Comparative Zoology as well as Director of the Peabody Museum of American Archeology and Ethnology, the writer came across an interesting comment on Rafinesque by David Starr Jordan. On a postal card mailed to Putnam from Indianapolis, Indiana, on January 10, 1876, is the message: "Dear Prof. Putnam, Rafinesque received. Many thanks. I find the old man's

descriptions are much better than he has been given credit for. Many thanks. D. S. Jordan." Undoubtedly that was not always the opinion of Jordan and unfortunately many other taxonomists in the fields of botany, ichthyology, and malacology have not enjoyed the same experience.

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Editor,
SYSTEMATIC ZOOLOGY:

Re Dr. Hyman's "How Many Species?" (*Syst. Zool., 4,* 142–143).

We are fully cognizant that inaccuracies exist in the preliminary chart of "The Relative Number of Living and Fossil Species of Animals," particularly with regard to the groups of animals on which there are divergent opinions on the number of living and fossil species.

We wish to repeat: "It is hoped that even in its incomplete form the compilation may prove to be of sufficient interest to fellow systematists to induce them to offer their critical comments and to contribute what basic data they may have on hand toward the improvement of the diagram."

We thank Dr. Hyman for the valuable information on nematodes.

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(*Concluded from p. 32*)

Faunal Distribution

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People and Projects

Dr. Zeno Payne Metcalf died suddenly and unexpectedly at his home at Raleigh, N. C., January 5, 1956, at the age of seventy. At the time of his death he was engaged in preparing a 42-volume catalog of the Homoptera of the world. Fifteen volumes had been or were in press at the time of his death, and several more volumes are nearly ready to go to press. An attempt is being made to provide means of completing the entire set of 42 volumes.

Dr. Metcalf was the author of 9 books and nearly a hundred professional publications. He was a key speaker at the International Congress of Zoology which convened in Paris in July, 1948, and at the International Congress of Entomologists which met in Stockholm in August, 1948. In addition he was president of 3 major national scientific organizations, the Entomological Society of America, the Ecological Society of America and the American Microscopical Society—a distinction accorded few scientists in the United States.

The University of Maryland announces the offerings of the Institute of Acarology for the Summer Session, 1956, from 16 July through 3 August. This program provides a unique opportunity for entomologists, parasitologists, zoologists, and advanced students in the field of biology to study the mites and ticks. The recent important discoveries of the role of the Acarina in the fields of public health and agriculture have emphasized the need for an understanding of all phases of knowledge concerned with mites and ticks. Their part in the epidemiology of the encephalitides, scrub typhus, "Q" fever, haemorrhagic fever, and other diseases, as well as their increased destruction of plants that has followed the introduction of the newer insecticides have brought them to the attention of an increasing number of biologists.

The staff this year consists of Edward W. Baker, U. S. Department of Agriculture; Joseph H. Camin, Chicago Academy of Sciences; Russell W. Strandtmann, Texas Technological College; and George Anastos and G. W. Wharton, of the University of Maryland. Further information can be obtained from G. Anastos, Department of Zoology, University of Maryland, College Park, Maryland.

The Tenth International Congress of Entomology will meet in Montreal from 17 to 25 August, this year. The meetings will be held at McGill University and at the University of Montreal. Although this Congress will be of interest primarily to entomologists, six of the fifteen sections will interest most systematic zoologists. These sections, in some of which symposia are being arranged, concern, respectively, systematics, behavior, ecology, geographical distribution, genetics and biometrics, and paleontology.

Inquiries about the Congress should be addressed to the Secretary of the Congress, J. A. Downes, Division of Entomology, Science Service Building, Ottawa, Ontario, Canada.

The Smithsonian Institution announces that an offset reprint of Charles Davies Sherborn's *An Index to the Genera and Species of the Foraminifera* [to 1889] is now available. Copies (485 pp.; clothbound) may be obtained from the Editorial and Publications Division, Smithsonian Institution, Washington 25, D. C. The price is $3.50, postpaid.

SYSTEMATIC ZOOLOGY is published quarterly by the Society of Systematic Zoology. Its purpose is threefold: To publish, and therefore to encourage the preparation of, contributions on basic aspects of all fields of systematics, principles and problems; to provide a suitable forum for discussion of the problems of the systematist and his methods; and to report as news the other activities of the Society of Systematic Zoology.

Contributions of the following types are solicited: Papers on principles and the applications of principles of wide implication and general interest in any phase of systematics, such as comparative anatomy, zoogeography, paleontology, taxonomy, classification, evolution, or genetics; discussions of methods, specific problems, and activities of systematists; discussions of new books and monographs; and news of systematists, organizations interested in systematics, research and teaching programs, expeditions, collections, meetings, and anything else of interest to systematists.

Consult recent issues for the style to be followed in the preparation of manuscripts. Contributors are encouraged to submit line drawings and diagrams to illustrate their articles. Half-tones may be accepted where necessary to the article.

Contributors receive galley proof but it is called to their attention that changes made in proof are expensive. The cost of alterations made in proof will be charged to the author if they exceed ten percent of the cost of composition.